PROC. R. SOC. VICT. vol. 98, no. 3, 97-119, September 1986

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS

6. THE GENERA *STROPHALOSIA* KING, 1844, *HETERALOSIA* KING, 1938 AND *ECHINALOSIA* WATERHOUSE, 1967.

By N. W. Archbold

Department of Geology, University of Melbourne, Parkville, Victoria 3052

Abstract: Strophalosiid brachiopods of the genera *Strophalosia, Heteralosia* and *Echinalosia* from the Permian sequences of Western Australia are revised and described. The new subgenus *Notolosia* is diagnosed and the following species described: *Strophalosia irwinensis* Coleman, *Strophalosia jimbaensis* sp. nov., *Heteralosia etheridgei* (Prendergast), *Heteralosia prendergastae* (Coleman), *Heteralosia complectens* (Etheridge), *Echinalosia prideri* (Coleman) and *Echinalosia* (*Notolosia*) *dickinsi* subgen. et sp. nov. Additional material belonging to *Strophalosia* and *Heteralosia* is briefly described and figured.

The classification of the superfamily Strophalosiacea is briefly discussed, the Ctenalosiinae of Muir-Wood and Cooper (1960) is raised to family status as the Ctenalosiidae and the new subfamily Licharewiellinae is proposed within the Strophalosiidae Schuchert (1913).

Strophalosiid brachiopods are abundant in the marine Permian faunas of Western Australia. This paper continues the series of studies on Western Australian Permian brachiopods (Archbold 1985) and documents representatives of the genera *Strophalosia, Heteralosia* and *Echinalosia*. The remainder of the Western Australian representatives of the family Strophalosiidae will be described in a subsequent study. Strophalosiids described herein come from various stratigraphical horizons within the Perth, Carnarvon and Canning Basins. The stratigraphy of these basins is documented in references referred to in Archbold (1981, p. 109) and the basis for age assignment of species is the same as that utilised in recent studies of Western Australian spiriferid brachiopods (Archbold & Thomas 1985). Terminology is standard as in previous studies.

Several of the species described are useful for interbasinal correlation, notably *Strophalosia irwinensis, Heteralosia etheridgei* and *Heteralosia complectens*, while all other species are useful for intrabasinal correlations.

The terminology used herein follows that used by Muir-Wood (1965) and Saryeheva (1970).

COLLECTIONS

All figured and measured specimens are housed in the following institutions as indicated by the prefix to the registered numbers. CPC—Commonwealth Palaeontological Collections of the Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T. GSWA—Geological Survey of Western Australia, Perth, Western Australia. MUGD—Department of Geology, University of Melbourne, Parkville, Victoria. UWA—Department of Geology, University of Western Australia, Nedlands, Western Australia. AMF—Australian Museum, Sydney, New South Wales.

All figured specimens of new species, other than holotypes are paratypes.

SYSTEMATIC PALAEONTOLOGY

Order Productida Sarycheva & Sokolskaya, 1959

Suborder Strophalosiidina Waterhouse, 1975

Superfamily Strophalosiacea Schuchert, 1913

Diagnosis: Strophalosiidinids with hinge teeth or denticles in the ventral valve and sockets in the dorsal valve. Ventral valve with well-developed interarea with pseudodeltidium closing delthyrium. Dorsal valve with low interarea. Ventral valve usually cemented by umbonal region and often with rhizoid spines on ears and slopes. Dorsal valve with or without spines. Cardinal process bilobed in primitive genera, trilobed in advanced genera. One family lacking interareas and teeth and sockets (Teguliferinidae).

Discussion: The diagnosis is largely based on Muir-Wood and Cooper's (1960) understanding of the Strophalosiidae. Waterhouse (1978a) included the Strophalosiidae Schuchert, 1913; Teguliferinidae Muir-Wood and Cooper, 1960; and the Hercosiidae Cooper and Grant, 1975 within the Strophalosiacea. It would appear preferable to leave the Hercosiidae within the Richthofeniacea as intended by Cooper and Grant (1975, p. 928) and the Teguliferinidae may also be better placed in the Richthofeniacea. Nevertheless the Teguliferinidae possess an erect "*Strophalosia*" type of cardinal process and a distinctive growth form of the ventral valve (Muir-Wood & Cooper 1960, p. 93). As a result I retain the family within the Strophalosiacea.

The subfamily Ctenalosiinae Muir-Wood and Cooper (1960) would appear to deserve family status, because of the distinctive development of ventral denticles and corresponding dorsal pits, and hence is raised to family status, as the Ctenalosiidae, herein. The Ctenalosiidae is diagnosed as Strophalosiacea with numerous ventral denticles and corresponding dorsal pits along the hinge. The genera *Ctenalosia* Cooper and

Stehli (1955) and *Mongolosia* Manankov and Pavlova (1976) are included within the family. The two genera are of strikingly-dissimilar external ornament and size and yet both possess dentieles and multiple soekets. The two genera do not appear elosely related and hence the origin of the Ctenalosiidae is obseure but it appears unlikely that the unusual dentieulate hinge line eould have evolved independently in the two genera.

Family Strophalosiidae Schuehert, 1913

Diagnosis: Strophalosiaeeans with ventral hinge teeth and dorsal soekets. Interareas distinet. Ventral valve usually eemented by umbonal region and often with rhizoid spines on ears and slopes. Dorsal valve with or without spines. Cardinal proeess bilobed, trilobed or quadrilobed.

Discussion: The subdivision of this family has been the subjeet of extensive diseussion. With the establishment of *Strophalosia gerardi* King, 1846 as the type speeies of *Strophalosia* King, 1844 (I.C.Z.N. 1962, Opinion 625), nomenelatural stability has oeeurred within the family. The morphologieal eharaeters of *Strophalosia gerardi* are diseussed under the generie heading.

Hall and Clarke (1892, p. 316) delineated stoeks of *Strophalosia* by means of the external ornament of the dorsal valve. They noted that there were speeies attributed to *Strophalosia* with spiniferous, lamellose or smooth dorsal valves. Muir-Wood and Cooper (1960) reeognised two subfamilies dependent on the nature of the dorsal exterior ornament: the Strophalosiinae Sehuehert with dorsal spines; the Heteralosiinae Muir-Wood and Cooper without dorsal spines. Beeause of the elarifieation of the morphology of the type speeies of *Strophalosia*, whieh laeks dorsal spines, Brunton (1966) redefined the Strophalosiinae as forms without dorsal spines and established the subfamily Dasyalosiinae Brunton for those genera with dorsal spines. This reeasting of subfamilies has been reviewed by Clarke (1970a) and Cooper and Grant (1975). Cooper and Grant (1975, p. 195) eonsidered *Heteralosia* to be generieally distinet from *Strophalosia*, a view adhered to herein, but they did not diagnose the distinetion. Irrespeetive of whatever eriteria are used to define subfamilies within the Strophalosiidae it appears diffieult to elassify *Heteralosia* and *Strophalosia* into separate subfamilies and henee the Heteralosiinae should be permitted to lapse. Grant (1976, p. 80) eontinued to use the Heteralosiinae without a diseussion of the arguments presented by Brunton (1966) and other authors or a comparison of *Heteralosia* with *Strophalosia*.

Waterhouse (1964, 1969) and Clarke (1970a) have aeerued data whieh questions the value of dorsal valve spinosity as a eriterion for subdividing the family. As a result I follow those authors in not employing dorsal valve spinosity as a eriterion for splitting the family. This is also eonsistent with views indieated by Grigor'eva (1977) and Chang and Ching (1976). For the present I ineludе the following subfamilies within the Strophalosiidae, namely Strophalosiinae Sehuehert, 1913; Mingenewiinae Arehbold, 1980 and Lieharewiellinae subfam. nov. The peeuliar nature of the Mingenewiinae was diseussed by Arehbold (1980b). The new subfamily Lieharewiellinae is formally proposed here and is diagnosed as Strophalosiidae with an external ornament of eourse eostae and variably-developed dorsal spines. Genera ineluded within the Lieharewiellinae are *Lieharewiella* Ustritskiy (in Ustritskiy *et al.* 1960), whieh is an objective senior synonym of *Costalosia* Waterhouse and Shah (1966), *Costalosiella* Waterhouse (1983) and *Australosia* MeKellar (1970). The presenee of eoarse eostae is a feature of all genera.

Lieharewiella was plaeed by Wang *et al.* (1966, p. 439) in the Aulostegidae Muir-Wood and Cooper, without discussion. Liao (1982, p. 539) ineluded *Lieharewiella* within his new subfamily Truneateninae within the Aulostegidae. However, deseription of Salt Range and Tasmanian *Lieharewiella* (ineluding the type speeies) by Waterhouse and Shah (1966) and Clarke (1970a) respeetively, indieates a firm strophalosiid affinity for the genus. The internal struetures of the Salt Range Lieharewiellinae are poorly known but Tasmanian evidenee (Clarke 1970a) indieates a firm strophalosiid relationship for the group.

Australosia MeKellar (1970) from the Latest Devonian of Queensland, possesses well-developed, eoarse, branching eostae on both valves and is possibly aneestral to Permian members of the subfamily.

Subfamily Strophalosiinae Sehuchert, 1913

Diagnosis: Strophalosiids with ventral valve normally eemented by umbonal region of ventral flank and often with rhizoid spines on ears and on flanks. Dorsal valve spinose, lamellose or smooth, may be eapillate and pitted. Cardinal proeess bilobed, trilobed or quadrilobed.

Discussion: This is a large subfamily of over 20 genera. The eonstituent genera have been well reviewed by Muir-Wood and Cooper (1960) or have been elearly diagnosed by subsequent authors. This paper deseribes representatives of the genera *Strophalosia* King (1844), *Heteralosia* King (1938) and *Echinalosia* Waterhouse 1967) from the Western Australian Permian. Relevant genera are compared with these genera below and additional Western Australian Permian Strophalosiinae will be deseribed in a subsequent paper.

Genus **Strophalosia** King, 1844

Type Species: *Strophalosia gerardi* King, 1846, from the Permian of Ladakh (Indian Himalayas), horizon unknown.

Discussion of Type Species: The holotype of the species (Galway University College, FC, D.267) has been figured by King (1850, pl. 19, figs 6-7), Davidson (1853, pl. 8, fig. 211), Hall and Clarke (1892, pl. 17, fig. 50), Prendergast (1943, pl. 5, figs 13, 16-17) and Brunton (1966, pl. 1, figs 8-9). Only Prendergast figured a profile of the holotype. Brunton also figured an additional speeimen from the Himalayas (1966, pl. 1, fig. 7), the speeimen having, presumably, also been eollected by Dr J. G. Gerard during his Himalayan expeditions.

The Himalayan expeditions of Surgeon J. G. Gerard of the Bengal Native Infantry resulted in several collections of fossils being sent down from the Himalayas. These fossils attracted considerable attention at the meetings of the Asiatic Society of Bengal with brief notes being written on some of the specimens and their locations (Everest 1831, 1833, Herbert 1831). Specimens were sent to England and commented upon briefly by J. deC. Sowerby (1832, 1833). Letters were also sent to the Asiatic Society by Gerard giving details of the fossil discoveries (Gerard, 1831) and who subsequently provided a large paper on the Spiti Valley region (Gerard, 1833). He was to have provided a second paper detailing the geological settings of his fossil discoveries (note to Gerard's 1833 paper by James Prinsep, Secretary to the Physical Class of the Asiatic Society of Bengal). However, the second paper does not seem to have eventuated. At least it is not referred to by Royle (1840), a valuable reference detailing much of the geological exploration of the Himalayas by that time. Royle (1840, pl. 3, figs 16-27) figured additional specimens collected by Gerard, one of which (op cit. pl. 3, fig. 23) may be allied to the Permian spiriferid genus *Trigonotreta*, again indicating that Gerard collected from Permian strata. For the time being the best indication of the locality of the type specimen is that given by Gerard (1833, p. 276-7) and repeated by King (1850, p. 96), namely "just before crossing the boundary of Ladakh into Basahir, I was gratified by the discovery of a bed of marine fossil shells resembling oysters, and clinging to the rock in a similar manner, but the suspicions of the Chinese prevented my bringing away many specimens. The loftiest position at which I actually picked up some of the shells was on the crest of a pass elevated 17,000 feet, where also were seen numerous blocks of calcareo-siliceous matrix" (Gerard 1833, p. 276-7). It is quite possible that other letters and perhaps maps were transmitted to the Asiatic Society of Bengal by Gerard and that an investigation of the old records of the society, if extant, may provide further information.

GENERIC DIAGNOSIS: Strophalosiinae with erect and recumbent spines over ventral valve. Dorsal valve with no spines, delicate concentric lamellae and delicate impersistent capillae. Shell shape usually subcircular.

DISCUSSION: The generic name *Strophalosia* was introduced by King (1844, 1845) and diagnosed later (1846, 1847). *Strophalosia gerardi* was described by King in 1846 and hence was the only species available as type species of the genus (I.C.Z.N. 1962, Opinion 625).

Coronalosia Waterhouse and Gupta (1978) (type species *Coronalosia blijniensis* Waterhouse & Gupta 1978) is morphologically closest to *Strophalosia*. It differs most obviously in the presence of a row of hinge spines that are sturdy and open into the interior of the valve into late maturity. Waterhouse and Gupta (1977, p. 14; 1983a, pp. 125) have used the name *Arclinaelosia*, a *nomen nudum*, which apparently refers to *Coronalosia*, a genus validly described in 1978.

Waterhouse and Gupta (1978, p. 417) noted that the dorsal exterior of *Strophalosia gerardi* is covered with prominent pits (or dimples) and pustules, as well as lamellae and traces of radial capillae and hence is similar to the dorsal valve of *Strophalosia subcircularis* Clarke (1970a) which is also covered with well-defined radial capillae according to those authors. Fine intermittent capillae occur on the dorsal valve of well-preserved specimens described herein and referred to *Strophalosia irwinensis* Coleman.

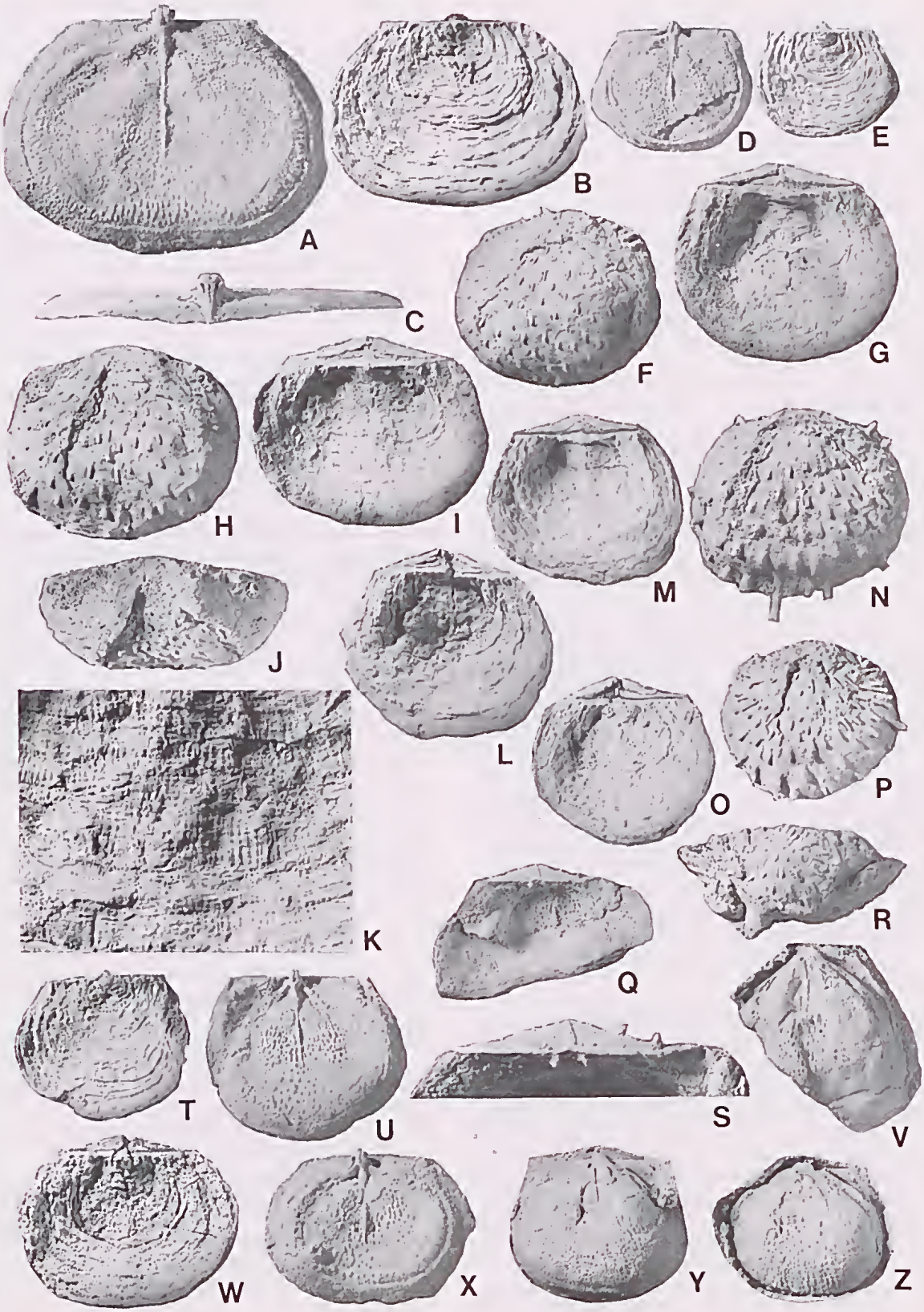
As noted by Brunton (1966), *Strophalosia* is similar morphologically to *Heteralosia* King 1938, a genus discussed below. Cooper and Grant (1975, p. 795) considered *Heteralosia* to be distinct from *Strophalosia*. However, they did not diagnose either genus. Their species *Strophalosia inexpectans*, is atypical for the genus *Strophalosia* and indeed the presence of fine, recumbent, hair-like spines on the dorsal valve precludes the species from *Strophalosia*. The species *Strophalosia inexpectans* possesses such delicate spines on both valves that it does not fit readily into any described strophalosiid genus. Grant (1976, p. 80) gave a detailed diagnosis of *Heteralosia* but did not compare the genus with *Strophalosia*. Nevertheless, *Heteralosia* is regarded herein as a distinct genus and is discussed further below.

Strophalosia is reliably known from early Permian faunas of Tasmania (Clarke, 1970a), New South Wales and Queensland (Waterhouse, *et al.* 1983) and Western Australia. Artinskian species are known from the Salt Range, Pakistan (in the forms of *S. tenuispina* Waagen, 1884 and *S. sublamellata* Reed, 1944). Late Permian species are known from the Himalayas (Waterhouse, 1983) and the Karakorum (Waterhouse & Gupta, 1983b), although, like *S. gerardi*, the age of which is not known, these species are relatively poorly known. Early Late Permian species such as *S. sibirica* Licharew (1934a) from northern and northeastern Siberia, Arctic USSR, appear to be true *Strophalosia* species (Grigor'eva, 1977). In the Soviet Arctic, the genus appears to occur as far west as Novaya Zemlya (Kalashnikov & Ustritskiy, 1981) and then as far south as the Kamian Priurals in the form of the Sakmarian *Strophalosia striatotuberculata* (Mirskaya *et al.* 1956).

Strophalosia irwinensis Coleman, 1957
Figs 1A-Z, 4A-I

1943 *Strophalosia* sp. cf. *gerardi*: Prendergast, p. 46; pl. 5, figs 14-15.
1943 *Strophalosia tenuispina*: Prendergast, p. 52; pl. 6, fig. 9.
1957 *Strophalosia (Heteralosia) irwinensis*: Coleman, p. 122; pl. 20, figs 1-6.
1957 *Strophalosia (Heteralosia) tenuispina*: Coleman, p. 130; pl. 20, figs 36-37.
1967 *Strophalosia prideri*: Condon, p.70
1976 *Strophalosia (Heteralosia) irwinensis*: Coleman; Playford *et al.*, p. 95.

HOLOTYPE: UWA 23441a, a ventral valve from Fossil Cliff, Irwin River; Fossil Cliff Member of the Holmwood Shale, Perth Basin. Figured by Coleman (1957, pl. 20, figs 1-2).


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z

MATERIAL, LOCALITIES AND AGE: Specimens as figured and measured in addition to abundant material from the Callytharra Formation collected by Dr G. A. Thomas, University of Melbourne. MUGD F6577, 6581, 6587, 3 isolated dorsal valves from G. A. Thomas locality PB 610, from measured section at 539 m bearing 290° from junction of Bilung Creek and Wooramel River, 75.5 m above base, Callytharra Formation. MUGD F6582, 6578, 6586, 2 conjoined shells and one ventral valve from G. A. Thomas locality PA 591, same section as above, 54.5 m above base, Callytharra Formation. MUGD F6590, an isolated dorsal valve from G. A. Thomas locality X813, from measured section, 2.5 km west of Coordewandy Homestead, at 8.5 m above base, Callytharra Formation. MUGD F6593, a conjoined shell from G. A. Thomas locality P 498, type section of Callytharra Formation, Callytharra Springs, 34-38 m above base of section. MUGD F6591, 6594, 1 conjoined shell and 1 isolated ventral valve from G. A. Thomas locality P 501, same section as P 498, 42-43 m above base of section. MUGD F6592, 6595, 2 conjoined shells from G. A. Thomas localities Q 550 and Q 545, from measured section on a creek near Gap Pool, Wooramel River, 4.6 km bearing 333° from Keogh Hill, Wooramel River District, 56 m and 42.5-46 m above base of section respectively, Callytharra Formation. All Carnarvon Basin. All Sterlitamakian (Late Sakmarian).

CPC 24429-24430, 2 ventral valve internal moulds from BMR locality TK5A, Scott Bluff, east side of Lake Blanche, southern Canning Basin, Cuncudgerie Sandstone. Sterlitamakian (Late Sakmarian).

Specimens from the Sterlitamakian Fossil Cliff Member of the Holmwood Shale (Perth Basin) were well figured by Coleman (1957, pl. 20, figs 1-6).

SIZE RANGES: A total of 44 specimens (including the figured specimens) were measured. Hinge width, 5.6-23.8 mm; maximum width, 7.5-32.8 mm; ventral valve height, 6.9-24.6 mm; dorsal valve height, 6.1-22.5 mm; thickness, 2.1-8.3 mm.

DIAGNOSIS: Small to medium sized *Strophalosia*; moderately-convex ventral valve; gently-concave dorsal valve in early stages of ontogeny, moderately-concave dorsal valve in maturity. Dorsal valve with ill-defined dimples, well-developed growth lamellae, radial capillae and no spines. Ventral valve with row of hinge spines and variably-defined rows of body spines; spines low angled and recumbent. Cicatrix of variable size.

DESCRIPTION: Shell small to medium sized, transversely oval or subcircular in outline. Hinge width varies from 0.6 of maximum width to 0.9 of maximum width. Hinge extremities rounded or finely pointed. Convexity of ventral valve relatively even with a slight increase in convexity over visceral disc. Gentle median depression or sulcus present in a few specimens but dies out before anterior margin of valve. Umbo not prominent, usually cemented to substrate. Cicatrix varies from small, barely recognisable to large (maximum size 10.9 mm wide), prominent; reflecting variable duration of attachment for juveniles of species. Dorsal valve flat to gently concave in juveniles, becomes more distinctly concave in mature individuals. Ventral interarea prominent, relatively high, gently concave or flat, finely-striated parallel to hinge line. Delthyrium small, high, narrow, filled with small, gently-convex pseudodeltidium. Dorsal interarea distinct, relatively high, bisected by small, narrow, high, triangular notothyrium filled by gently-convex chilidium. Dorsal interarea inclined at up to 30° to cardinal process or may be close to coplanar with the process.

Ornamentation of ventral valve consists of scattered spines, at times showing concentric and subquincuncial arrangement. Spines relatively coarse along cardinal margin and anterior portion of mature specimens, being up to 1 mm thick at bases. Body spines vary from recumbent to projecting anteriorly at low angle to valve. Hinge spines erect, point away from umbo; arranged as single row along cardinal margin and over ill-defined, small ears. Ventral valve also possesses widely-spaced, distinct, concentric growth lamellae.

Dorsal valve lacks spines but possesses prominent, concentric growth lamellae, low, fine, radial capillae between the lamellae (about 3 per mm at 1.8 cm from umbo) and a few scattered, shallow, elongate dimples on a minority of specimens. Many specimens lack dimples entirely.

Ventral interior possesses distinct, but small, diverging teeth. Muscle marks clearly shown on internal moulds; adductor scars relatively small, smooth and bisected by low ridge. Diductor scars large, flabellate, smooth or gently striated. Low marginal ridge may be developed around perimeter of ventral interior. Remainder of ventral visceral disc carries fine pustules and indistinct striations. Trail of valve smooth interiorly.

Fig. 1—A-Z, *Strophalosia irwinensis* Coleman. A-X, from Callytharra Formation, Carnarvon Basin; Y-Z, from Cuncudgerie Sandstone, Canning Basin. A-C, MUGD F6577, dorsal valve in ventral, dorsal and posterior views, × 2, × 1.6 and × 2.3 respectively. D-E, MUGD F6581, dorsal valve in ventral and dorsal views, × 2 and × 1.8 respectively. F-G, MUGD F6582, shell in ventral and dorsal views, × 1.3 and × 1.4 respectively. H-K, MUGD F6578, shell in ventral, dorsal and posterior views, × 1.2, enlargement of part of dorsal valve exterior, × 5.5. L, MUGD F6583, shell in dorsal view, × 1.6. M-N, MUGD F6584, shell in dorsal and ventral views, × 1.5 and × 1.8 respectively. O-P, MUGD F6585, shell in dorsal and ventral views, × 1.8. Q-S, MUGD F6586, ventral valve in dorsal and posterior views, × 1.4, enlargement of ventral interarea, × 3. T-U, MUGD F6587, dorsal valve in dorsal and ventral views, × 1.8 and × 2.2. V, MUGD F6588, ventral valve internal mould, × 1.6. W, MUGD F6589, shell in dorsal view, × 1.6. X, MUGD F6580, dorsal valve in ventral view, × 2. Y, CPC 24429, ventral valve internal mould, × 1.3. Z, CPC 24430, ventral valve internal mould, × 1.6.

Dorsal valve interior carries strong median septum; arises from cardinal process, extends some two-thirds of valve length. Adductor muscle scars smooth, in two pairs, with anterior pair most prominent. Muscle scars bisected by median septum. Cardinal process erect, inclined up to 60° to plane of visceral disc. Exteriorly cardinal process trilobed, in mature individuals, with central lobe being most prominent. Interiorly, cardinal process appears quadrilobed with large central lobe being gently bisected by gentle depression and a smaller lateral lobe occurring each side of central lobe. Anterior of interior of dorsal valve sharply turned into short trail.

Discussion: This species has been well described by Coleman (1957) and additional, large collections from the Callytharra Formation, upon which the above description was based, confirms the essential details of his description. *S. irwinensis* can now be confidently assigned to *Strophalosia* following the elucidation of the type species by Muir-Wood and Cooper (1960), Waterhouse (1964) and particularly Brunton (1966).

S. gerardi King (1846), from the Permian of the Himalayas, is a larger species than *S. irwinensis* and possesses prominent elongate dimples on the dorsal valve exterior and more numerous spines on the ventral valve (Brunton 1966, pl. 1, figs 8, 9). The umbonal shoulders of *S. gerardi* are much more prominent than those of *S. irwinensis*.

S. subcircularis Clarke (1970a) and its variants is a relatively large species with a cicatrix that may vary considerably in size (e.g. Clarke 1970a, pl. 1, fig. 6a) like that of *S. irwinensis*. The early Permian (Sakmarian) Tasmanian species is strongly convex with a variably-dimpled dorsal valve.

The Late Permian *S. diadema* (Waterhouse & Gupta 1983b) from the Southern Karakorum is a larger species with a shallow median sulcus but is only known from a few specimens and the illustrations of the species are not clear. Specimens attributed to *S. gerardi* by Waterhouse (1983, pl. 1, figs 1-2) from the Late Permian of Nepal are small and the dorsal exterior possesses irregular growth lamellae when compared with that of *S. irwinensis*. Comparison of *S. irwinensis* with *S. jimbaensis* sp. nov. is given under that species.

Both Prendergast (1943) and Coleman (1957) referred one imperfectly-preserved ventral valve from the Fossil Cliff Member to *Strophalosia tenuispina* Waagen (1884) but as noted by Coleman (1957, p. 131) the specimen could "equally as well belong to other species, in particular . . . *S. irwinensis*". The specimen is now formally referred to *S. irwinensis* in the interests of nomenclatural stability.

Strophalosia jimbaensis sp. nov.
Fig. 2A-G

Holotype: CPC 24405, a conjoined shell from the type section of the Jimba Jimba Calcarenite, Carnarvon Basin.

Material, Localities and Age: The four available specimens (all conjoined shells, 2 incomplete) are from the type section of the Jimba Jimba Calcarenite (Lat. 25°02′75″S; Long. 114°58′5″E), Jimba Jimba Station, 15 km west of Jimba Jimba Homestead (Condon 1967, p. 89), Carnarvon Basin. MUGD F6596-6598 come from 16.5 m above the base of the section. All specimens are Aktastinian (Early Artinskian).

Measurements (in mm): * = holotype, e = estimate

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness	Height ventral interarea
CPC 24405*	18.7	37.2	31.8	28.0	8.2	1.8
MUGD F6596	20.0c	32.0c	27.5	24.6	–	2.4
MUGD F6597	23.0	38.0	26.5+	23.5+	10.7	2.8
MUGD F6598	19.2	34.6	–	–	11.5	2.0

Diagnosis: Medium- to large-sized *Strophalosia*; moderately convex ventral valve; concave dorsal valve. Dorsal valve with well defined dimples, growth lamellae and radial capillae, no spines. Ventral valve with hinge spines, two rows on ears, numerous scattered sub-erect body spines and a shallow median sulcus.

Description: Shell medium- to large-sized, transversely oval in outline. Hinge width varies from about 0.5 of maximum width to 0.65 of maximum width (based on small collection). Hinge extremities rounded. Convexity of ventral valve relatively even judged from available specimens. Gentle median sulcus developed in ventral valve, persists until anterior margin of shell. Umbo small, weakly pointed; cicatrix small, extends from umbo for only a few mm. Dorsal valve gently concave at juvenile stages of ontogeny, becomes more distinctly concave in mature individuals. Ventral interarea prominent, flat, finely striated parallel to hinge line. Delthyrium small, high, narrow, filled with small, gently convex pseudodeltidium. Dorsal interarea distinct, relatively high; bisected by narrow, high, triangular notothyrium filled by gently convex chilidium.

Dorsal valve lacks spines but possesses prominent, concentric growth lamellae, low, fine, radial capillae between lamellae (about 3 per mm at 1.5 cm from umbo) and numerous scattered to subquincuncially arranged, circular to slightly elongate dimples (or pits).

Interior structure of the species not known.

Discussion: This species is described and named formally because of its larger size, shallow ventral sulcus and

Fig. 2-A-G—*Strophalosia jimbaensis* sp. nov. A-G, from Jimba Jimba Calcarenite, Carnarvon Basin. A-B, CPC 24405, holotype, shell in dorsal and ventral views, × 1.1. C, MUGD F6596, crushed shell in dorsal view, × 1.2. D-F, MUGD F6597, shell in dorsal, ventral and posterior views, × 1.1. G, MUGD F6598, incomplete shell in dorsal view, × 1.2. H-O, *Strophalosia* sp. cf. *S. jimbaensis* sp. nov., all from One Gum Formation, Carnarvon Basin. H, CPC 24431, natural cast of ventral valve in ventral view, × 1.2. I, CPC 24435, natural cast of dorsal valve, interior view, × 1.2. J, CPC 24433, natural cast of ventral valve in ventral view, × 1.2. K, CPC 24434, natural cast of ventral valve in ventral view, × 1.2. L, CPC 24432, natural cast of ventral valve in ventral view, × 1. M, CPC 24436, natural cast of dorsal valve, interior view, × 1. N, CPC 24437, natural cast of dorsal valve in dorsal view, × 1.2. O, CPC 24438, natural cast of ventral valve, interior view, × 1.2.


A
B
C
D
E
G
F
H
I
J
K
L
M
N
O

strongly dimpled dorsal valve which collectively characterise a distinctive form. Nevertheless, further collections will add to the variation of the species and enable the elucidation of the internal structures.

S. jimbaensis sp. nov. is readily distinguished from *S. irwinensis* by means of the distinctive features of the species. *S. jimbaensis* sp. nov. is closer to both *S. gerardi* King and *S. subcircularis* Clarke in details of size, outline and spinosity but both the Himalayan and Tasmanian species appear to lack the distinctive shallow ventral sulcus and neither species possesses such well-developed dorsal valve dimples.

Strophalosia sp. cf. **S. jimbaensis** sp. nov.
Fig. 2H-O

MATERIAL, LOCALITIES AND AGE: CPC 24431-24435, four natural casts (in ferruginous siltstone) of ventral valves and 1 natural cast of a dorsal valve from BMR locality WB 9, 2 km on a bearing of 285° from Keogh Hill, One Gum Formation. CPC 24436-24438, 2 natural casts of dorsal valves and 1 natural cast of a ventral valve (all in ferruginous siltstone) from BMR locality 78, 64, 042, 7, Glenburgh Run 13A, Photo 5009, 2.4 km at 276° from Keogh Hill, collector Dr J. M. Dickins, base of One Gum Formation. All Carnarvon Basin. All Aktastinian (Early Artinskian).

MEASUREMENTS (in mm): Measurements are rounded off because preservation does not permit accuracy to one decimal place. e = estimate.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness
CPC 24431	–	38	32	–	9.0e
CPC 24433	–	35	35	–	11.0e
CPC 24434	–	39	33	–	–
CPC 24435	23	41	–	32	–
CPC 24437	21	39	–	29	–
CPC 24438	–	40+	38	–	–

DIAGNOSIS: Large *Strophalosia*. Ventral valve moderately convex with hinge spines, numerous scattered body spines and a shallow median sulcus. Dorsal valve concave with well-defined dimples, no spines.

DESCRIPTION: Shell large, transversely oval in outline. Convexity of ventral valve relatively even, no increase in convexity over visceral region. Gentle median sulcus developed in ventral valve, persists until anterior of shell. Dorsal valve gently concave.

Ornamentation of ventral valve consists of coarse scattered spines at times showing concentric and subquincuncial arrangement. Spine bases up to 1.0+ mm thick. Body spines semi-erect or recumbent—the better preserved specimens indicate they were primarily semi-erect. Numerous spines developed over small ears. Relationships of spines not clear but appears to be at least two rows present (spines spaced at 1-1.5 mm intervals adjacent to ears and at 2-3 mm intervals elsewhere on valve).

Dorsal valve lacks spines but possesses prominent concentric growth lamellae and distinct, circular to slightly elongate dimples.

Ventral valve interior carries smooth adductor scars, posteriorly located, bisected by low ridge. Diductor scars less well impressed, appear large, flabellate, striate.

Dorsal valve interior with distinct median septum, arising from cardinal process (details unknown). Low to prominent marginal ridge present. Brachial ridges poorly known.

DISCUSSION: The specimens discussed are closest to *S. jimbaensis* sp. nov. in details of ventral valve morphology and dorsal valve exterior ornament but information on the nature of the cardinal area of the One Gum Formation specimens and the internal morphology of *S. jimbaensis* sp. nov. is required for a confident referral of the material at hand to that species. Nevertheless the two occurrences appear to be closely related. The present material is distinct from other species of *Strophalosia* on similar grounds to those discussed for *S. jimbaensis*.

Genus **Heteralosia** King, 1938

TYPE SPECIES: *Heteralosia slocomi* King, 1938.

DIAGNOSIS: Small Strophalosiinae with erect and recumbent spines over ventral valve. Dorsal valve with no spines but with concentric lamellae, usually non-capillate. Delthyrium filled by dorsal cardinal process when valves closed and/or narrow pseudodeltidium. Outline of shell rounded, usually with small ears. Brachial ridges often weakly developed.

DISCUSSION: As noted by Clarke (1970a, p. 21), although the original diagnosis of *Heteralosia* was based on a false premise (that the type species of *Strophalosia* was a species with a spinose dorsal valve) there appears to be good evidence for the validity of the genus. Nevertheless the genus is close to *Strophalosia* s.s. and it can be noted that King (1938) placed *Strophalosia gerardi* in his genus. It would appear that many species of *Heteralosia* spent most if not their entire life permanently attached to a supporting object. Species of *Strophalosia* were apparently well detached by maturity. However, size of the cicatrix is not a guide to a particular species duration of attachment. The largest specimen of *Strophalosia irwinensis* described herein happens to possess the largest cicatrix of any specimen of the species seen by the author but that species shows a wide variation in cicatrix size. Coleman used the size of the cicatrix as one of his criteria for recognition of species within *Heteralosia* and hence not surprisingly, species of the genus appeared to range throughout almost the entire Permian sequence of Western Australia. Clarke (1970a) considered that *Heteralosia* was characterised by weak brachial ridges as did Grant (1976). However, illustrations of various species of *Heteralosia* from the Glass Mountains provided by Cooper and Grant (1975) reveal many individuals with well-developed brachial ridges. Some specimens of *H. etheridgei* described herein also possess clearly-developed brachial ridges.

Waterhouse (1959, 1964, 1969, 1981) has repeatedly drawn attention to the need for a consideration of the ontogeny of strophalosiid shells when describing strophalosiid species. As a result he and Brunton (1966)

have queried the validity of *Heteralosia*. Nevertheless, the observation that some specimens of species such as *H. etheridgei* possess well-developed brachial ridges (which the present author considers to be a feature of adult or, at least, submature shells) leads to the conclusion that two groups of strophalosiids with non-spinose dorsal valves occur in the Western Australian Permian faunas. Attempts have been made herein to discriminate between juvenile *Strophalosia irwinensis* and mature *Heteralosia etheridgei*. As a result the present author agrees with Clarke (1970a) and Grant (1976) that *Heteralosia* is a useful generic concept. However, Waterhouse (1959) has clearly established the importance of ontogenetic studies in the group.

Both Prendergast (1943) and Coleman (1957) confused the productacean genus *Etheridgina* Oehlert with small attached strophalosiids. The productacean characters of *Etheridgina*, well shown by Etheridge (1876, 1878) and Oehlert (1887) were confirmed by the modern studies of Waterhouse (1959) and Muir-Wood and Cooper (1960). Prendergast (1943) and Coleman (1957) were apparently confused by Etheridge's (1918) use of the trivial name *complectens* for his new species of *Strophalosia*. Etheridge, of course, did not refer to his previous use of the trivial name *complectens* for his "*Productus*" (i.e. *Etheridgina*) as the two species were not related. The suppression of the binomen *Strophalosia complectens* by both Prendergast and Coleman is not justified and hence the name is restored herein. Greger's (1920) erroneous treatment of *Etheridgina* undoubtedly added to the confusion for subsequent authors. Prendergast (1943, p. 53) appears to have examined and misinterpreted specimens of *Etheridgina* from Scotland.

Heteralosia etheridgei (Prendergast, 1943)
Fig. 3A-Z, AA-BB

1943 *Strophalosia* cf. *Strophalosia beecheri*: Prendergast, p. 41, pl. 5, figs 1-3.
1943 *Strophalosia etheridgei* Prendergast, p. 43, pl. 5, figs 5-12.
1943 *Strophalosia* sp. ind. A. Prendergast, p. 51, pl. 6, figs 10-12.
1957 *Strophalosia* (*Heteralosia*) *etheridgei* Prendergast, Coleman, p. 120, pl. 19, figs 30-32.
1957 *Strophalosia* (*Heteralosia*) *prendergastae* Coleman (partim.), p. 127, pl. 20, figs 25-28 (non cet.).

Lectotype: GSWA 1/5252a, figured by Prendergast (1943, pl. 5, figs 6, 7) from creek 0.8 km (0.5 mile) west of Callytharra Springs, Wooramel River, Carnarvon Basin. Callytharra Formation. Chosen by Coleman (1957, p. 120).

Material, Localities and Age: Specimens as figured and measured in addition to abundant material from the Callytharra Formation, collected by Dr G. A. Thomas, University of Melbourne. MUGD F6599-6602, 4 isolated dorsal valves from G. A. Thomas locality Q545, from measured section on a creek near Gap Pool, Wooramel River, 4.6 km bearing 333° from Keogh Hill, Wooramel River district, 42.5-46 m above base of section, Callytharra Formation. MUGD F6603, 1 isolated ventral valve from G. A. Thomas locality Q550, same section as above, 56 m above base of section. MUGD F6604, 1 isolated ventral valve from G. A. Thomas locality Q556, same section as above, 42.5-57 m above base of section. MUGD F6605, 1 isolated ventral valve from G. A. Thomas locality Q559, same section as above, 76 m above base of section. MUGD F6606, 6607, 1 isolated dorsal valve and 1 conjoined shell from G. A. Thomas locality P498, type section of Callytharra Formation, Callytharra Springs, 34-38 m above base of section. MUGD F6579, 1 isolated dorsal valve from G. A. Thomas locality P495, same section as above, 33 m above base of section. CPC 24406, 24439, 24440, 3 conjoined shells from BMR locality GW87, type section of Callytharra Formation, Callytharra Springs, 10-17 m above base of section. All Carnarvon Basin.

GSWA F270, external mould of dorsal valve from Fossil Cliff, Irwin River District, Perth Basin, Fossil Cliff Member of the Holmwood Shale. A ventral valve from the Fossil Cliff Member was figured by Coleman (1957; pl. 19, figs 27-28).

All Sterlitamakian (Late Sakmarian).

Size Ranges: A total of 22 specimens (including the figured specimens) were measured. Hinge width, 3.3-9.5 mm; maximum width, 4.6-12.9 mm; ventral valve height, 5.0-13.0 mm; dorsal valve height, 4.0-10.8 mm; thickness, 2.0-6.2 mm; ventral interarea height, 0.5-1.4 mm; dorsal interarea height, 0.2-1.2 mm.

Diagnosis: Small *Heteralosia*; elongate to circular outline. Cicatrix often small, in a few specimens relatively large. Exterior ornament of pronounced concentric lamellae and widely spaced, usually relatively-coarse, ventral spines. Dorsal exterior with fine capillae and scattered, widely-spaced dimples.

Description: Shell small, elongate oval to circular in outline. Hinge width varies from two-thirds to over seven-eighths maximum width. Hinge extremities usually finely pointed in mature specimens. Small ears, poorly demarcated from rest of shell, may be developed. Juvenile specimens with hinge extremities more rounded. Ventral valve strongly convex with convexity decreasing anteriorly. Maximum width at about mid-length of shell. Umbo invariably flattened, carries distinct cicatrix of attachment, usually small in size, but, in a few specimens, attaining relatively large size (the two largest measured: Specimen MUGD F6605, 6 mm wide, 4 mm long; Specimen MUGD F6607, 5 mm wide, 3.5 mm long). Ornamentation of ventral valve consists of spines and concentric lamellae. Spines distributed as row along hinge, when cicatrix small, and moderately to widely spread along concentric rows over valve. Spines may be spaced at intervals of 3 mm or more, in which case specimen may have relatively few spines (e.g. Specimen CPC 24406 has some 27 spines), or at about 2 mm intervals. Spines relatively coarse (e.g. up to 0.6 mm thick on specimen CPC 24440), tend to be adherent posteriorly, suberect anteriorly.

Interareas distinct, flat, extend full width of hinge, relatively low. Ventral interarea striated parallel to hinge, bisected by narrow triangular delthyrium filled by


A
B
C
E
F
D
G
H
L
K
J
M
I
O
N
P
Q
S
T
R
U
V
W
Z
X
Y
AA
BB

weakly-convex pseudodeltidium. Dorsal interarea about half to two-thirds height of ventral interarea, weakly striate parallel to hinge line, bisected by triangular, flat to weakly-convex, chilidium.

Dorsal valve flat or gently convex during earliest stages of ontogeny, then becomes increasingly concave anteriorly and tends to be distinctly geniculated in front of visceral disc. Concentric lamellae distinct exteriorly; when well preserved may carry fine capillae (some 3 to 4 per mm on Specimen CPC 24406). Spines absent.

Ventral teeth small, divergent. Marginal ridge, arising near teeth may continue laterally, demarcating small ears clearly, then die out on lateral margins of valve. Adductor scars situated high up under umbo on small raised platform; diductor scars poorly impressed, weakly striate. Anterior of interior of ventral valve smooth.

Cardinal process arises from strong median septum and two, small lateral ridges which surround small, deep sockets. Process spike-like, extending posteriorly at small angle to plane of dorsal interarea; its interior face bilobed in juvenile specimens (because of a pronounced groove bisecting the single, large lobe), quadrilobed in mature specimens with small lateral lobes becoming developed.

Smooth dorsal adductor scars distinct, particularly in mature specimens; often raised above level of visceral disc; bisected by median septum, not differentiated into anterior and posterior components. Median septum usually slightly more than half valve length, raised anteriorly. Abundant papillae occur around anterior of valve. Brachial ridges variably developed but some specimens show distinct, typical, strophalosiid brachial ridges.

Discussion: Specimens at hand modify the understanding of this species from that given by Prendergast (1943) and Coleman (1957). The cicatrix of attachment may vary considerably in size and this, in turn, may impart a distorted outline to some specimens. For these reasons a Callytharra specimen previously referred to *H. prendergastae* by Coleman (1957) is now referred to *H. etheridgei*, as discussed under *H. prendergastae*. Spinosity varies more than allowed for by Coleman (1957) although ventral spines are apparently never as dense as those of *H. prendergastae*. One specimen (MUGD F6604) possesses the typical spine pattern of the species but is unusual in that the spines are fine (only being 0.3 to 0.4 mm wide); it is presumed to be a variant of the species.

H. etheridgei is close to *H. prendergastae* but is differentiated from that species by a less densely spinose ventral valve and a dorsal valve with well developed concentric lamellae and only rarely with dimples. On average *H. etheridgei* is a smaller species than *H. prendergastae*.

Juveniles of *Strophalosia irwinensis* are close to *H. etheridgei* but invariably possess a less-convex ventral valve (at comparable sizes) and often have a larger flat cicatrix of attachment. Juveniles of *S. irwinensis* also tend to be more transverse in outline than *H. etheridgei* and to have more closely-spaced, finer, ventral spines. Juvenile *S. irwinensis* are measured and figured in a discussion of that species.

The *Strophalosia rarispina* of Mansuy (1914) from Phnom Ta Maol, Cambodia (Mansuy 1914, pl. 2, figs 9a-d) has a strongly-developed ventral convexity, small umbonal cicatrix and elongate outline that recall *H. etheridgei* but the Cambodian shell has a very low ventral interarea.

H. haerens Grant (1976, p. 83, pl. 18, figs 1-28) is also moderately close to *H. etheridgei* but is distinguished from the Western Australian species by its normally larger cicatrix of attachment and lack of pseudodeltidium. The Thailand species, from the Late Early Permian, is also much smaller than *H. etheridgei*.

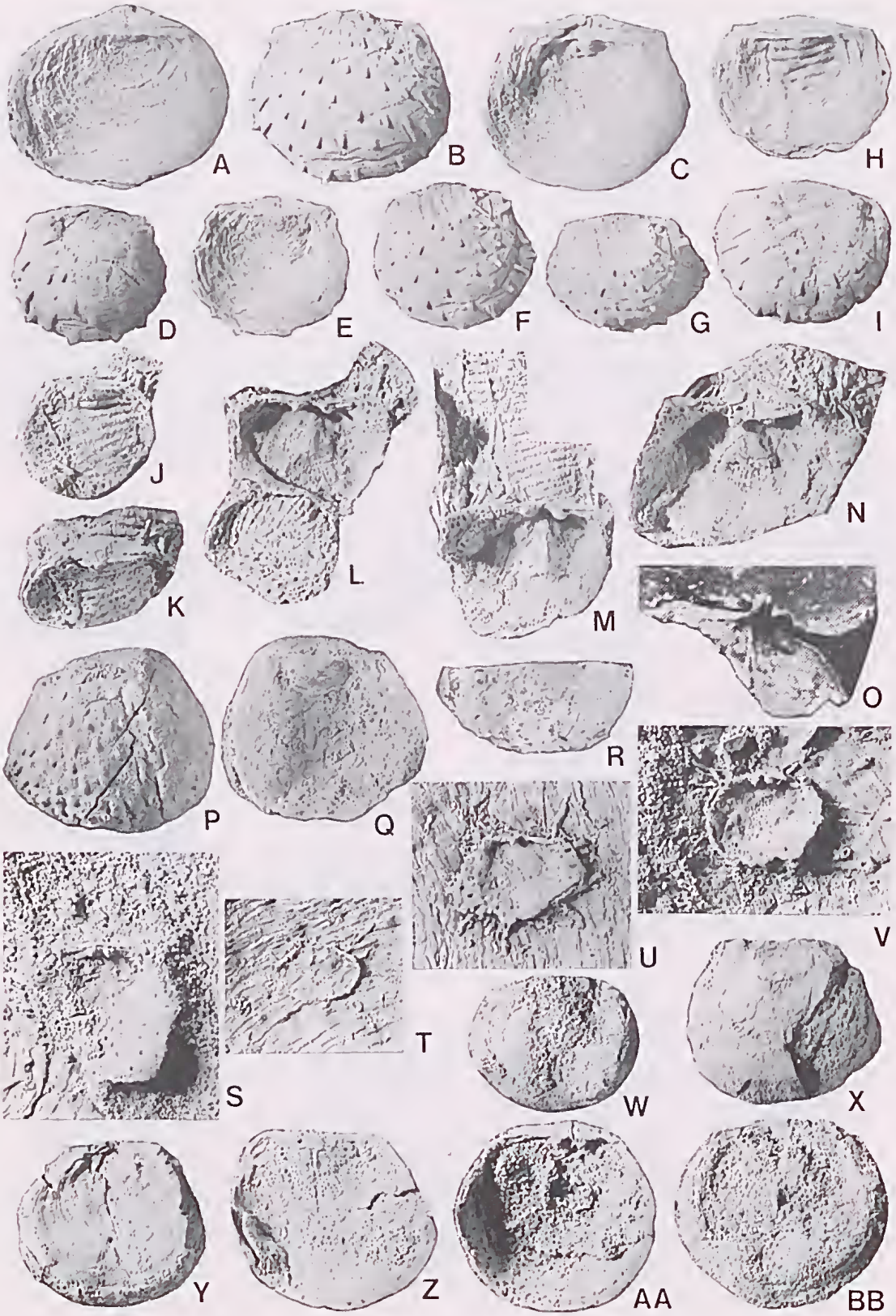
Heteralosia prendergastae (Coleman, 1957)
Fig. 4P-R

1957 *Strophalosia* (*Heteralosia*) *prendergastae* (Coleman (partim.), p. 127; pl. 20, figs 20-24 (non cet.)

Holotype: UWA 28444a, a conjoined shell from the Cundlego Formation, Carnarvon Basin.

Material, Locality and Age: Only the holotype of the species is known; the paratype (UWA 28444b) cannot be located in the UWA collections. The type locality is: 350 yards (approx. 320 metres) west of fence between Barabiddy and Weer Paddocks, 2220 yards (approx. 2 km) south of gate in that fence, near Barabiddy Creek, south of Wandagee Homestead, Carnarvon Basin, Cundlego Formation. Late Baigendzhinian (Late Artinskian).

Fig. 3—A-Z, AA-BB, *Heteralosia etheridgei* (Prendergast). A-Z, AA, from Callytharra Formation, Carnarvon Basin; BB, from Fossil Cliff Member, Perth Basin. A-B, MUGD F6599, dorsal valve in ventral and dorsal views, × 3.5. C-D, MUGD F6600, dorsal valve in ventral and dorsal views, × 3.5. E-F, MUGD F6601, dorsal valve in ventral and dorsal views, × 4. G-H, MUGD F6606, dorsal valve in ventral and dorsal views, × 4 and × 3.5 respectively. I, MUGD F6604, ventral valve in ventral view, × 2.6. J, MUGD F6579, dorsal valve in ventral view, × 4.5. K-M, CPC 24406, shell in posterior, dorsal and ventral views, × 3.5, × 3 and × 3.5 respectively. N-P, MUGD F6607, shell in dorsal, ventral and posterior views, × 3.2, × 3.8 and × 3.8 respectively. Q-R, MUGD F6603, ventral valve in ventral and dorsal views, × 4.5 and × 3.8 respectively. S-T, CPC 24439, shell in ventral and dorsal views, × 4.5 and × 3 respectively. U-W, CPC 24440, shell in ventral, posterior and dorsal views, × 4, × 4 and × 3 respectively. X-Y, MUGD F6605, ventral valve in ventral and dorsal views, × 3.5. Z, AA, MUGD F6602, dorsal valve in ventral and dorsal views, × 3.6. BB, GSWA F270, external mould of dorsal valve, ×3.5.


A
B
C
H
D
E
F
G
I
J
L
M
N
K
O
P
Q
R
V
U
S
T
W
X
Y
Z
AA
BB

MEASUREMENTS (in mm): Measurements of the paratype are from Coleman (1957). * = holotype.

Specimen	Hinge width	Maximum width	Ventral height	Dorsal height	Thickness	Height ventral interarea
UWA 28444a*	7.5	12.5	'1.5	10.3	4	1.1
UWA 28444b	7.5	13.5	15.7	–	5	–

DIAGNOSIS: Small *Heteralosia*, not attached as adults, with numerous fine ventral spines and irregularly-dimpled dorsal exterior. Cicatrix prominent.

DESCRIPTION: Shell small with subcircular outline. Cicatrix distinct, may distort outline posteriorly. Cicatrix flat, arises on umbo, hence umbo not clearly demarcated. Anterior of cicatrix, ventral valve evenly, strongly convex. Transversely, lateral slopes steep; middle of ventral valve less convex, no sulcus present. Hinge line straight, about 0.6 of maximum shell width. Maximum shell width at mid length of shell. No distinct ears present. Ventral interarea low, bisected by narrow, triangular delthyrium filled with slightly-convex pseudo-deltidium.

No spines on cicatrix. Remainder of ventral valve covered with numerous fine, spine bases, often elongated, that give rise to recumbent or semi-erect spines. Spine bases fine, none exceed 0.5 m in width; arranged in semiquincuncial manner. No growth lamellae on ventral valve.

Dorsal valve moderately concave. Initial part of valve flat; anteriorly, valve becomes evenly concave, flattening towards anterior margin. Dorsal interarea low, bisected by small, distinct chilidium. Valve exterior aspinose, growth lines poorly developed. Valve exterior carries numerous, randomly scattered dimples.

Interior of shell unknown.

DISCUSSION: This species is one of the least well-known strophalosiid species from the Western Australian Permian. Coleman (1957) indicated a wide stratigraphic range for the species (Sterlitamakian to Chhidruan as used herein) and this requires substantial reappraisal. Several of his specimens were from the Hardman Formation of the Canning Basin. These (Coleman 1957, pl. 20 figs 29-35) can confidently be assigned to *Echinalosia* (*Notolosia*) *dickinsi* subgen et. sp. nov. described below; they have been well figured by Coleman and are characteristic of the new subgenus and species. *H. prendergastae* was also recorded by Coleman (1957, pl. 20, figs 25-28) from the Callytharra Formation. The Callytharra specimen is referred by me to *H. etheridgei* Prendergast; it is partly decorticated and hence does not clearly display the coarser, more numerous spines of the holotype of *H. prendergastae* and it also possesses more well-developed dorsal growth lamellae as in *H. etheridgei*. Coleman (1957) categorised his species by its more numerous, fine spines (but coarser than those of *H. etheridgei*), larger size, more quadrate outline and large cicatrix of attachment. However, new collections of *H. etheridgei* show that the species can be larger than previously realised and that the cicatrix of attachment varies in size for the species (although it does not often appear to be as large as that of the holotype of *H. prendergastae*). Difficulties of distinguishing between *H. etheridgei* and juveniles of *Strophalosia irwinensis* are discussed under *H. etheridgei* but Coleman's Callytharra specimen is more circular to elongate and strongly ventrally convex than is normal for juvenile *S. irwinensis*. The revision of *H. etheridgei* given above indicates that *H. prendergastae* is better characterised by its more numerous ventral spines and a dorsal exterior with no distinct growth lamellae and an irregularly dimpled surface. Nevertheless large collections from the Cundlego, and possibly Wandagee Formations are required to place the species on a firm understanding.

H. prendergastae is probably closely related to *H. iphia* Grant (1976, p. 84, pl. 18, figs 29-50) from the Late Early Permian of Thailand. Grant's species possesses numerous ventral spines, a distinct cicatrix and a dorsal exterior with irregularly-scattered dimples and variably-developed growth lamellae.

Heteralosia compleetens (Etheridge, 1918)
Fig. 4J-O

1915 *Strophalosia* sp. Etheridge, p. 34; pl. 5, figs 16-18
1918 *Strophalosia complectens* Etheridge, p. 253; pl. 40, figs 11-12
1926 *Strophalosia complectens* Etheridge; Glauert, p. 46
1943 *Etheridgina muirwoodae* Prendergast, p. 54; pl. 6, figs 14, 15
1957 *Etheridgina*(?) *muirwoodae* Prendergast; Coleman, p. 109; pl. 17, figs 6-11
1958 *Etheridgina*(?) *muirwoodae* Prendergast; Guppy *et al.*, p. 48

Fig. 4—A-I, *Strophalosia irwinensis* Coleman. A-I, from Callytharra Formation, Carnarvon Basin. A, MUGD F6591, shell in dorsal view, × 3. B-C, MUGD F6592, shell in ventral and dorsal views, × 3. D-E, MUGD F6593, shell in ventral and dorsal views, × 3.6. F-G, MUGD F6594, ventral valve in ventral and posterior views, × 3. H-I, MUGD F6595, shell in dorsal and ventral views, × 3. J-O, *Heteralosia complectens* (Etheridge). All from Noonkanbah Formation, Canning Basin. J-K, AMF16699a, lectotype, shell in dorsal and posterior views, × 3. L, AMF16812, ventral valve and incomplete shell in dorsal views, × 3. M, AMF16699b, ventral valve in ventral view, × 2.6. N, AMF16699c, ventral valve in ventral view, × 2.6. O, missing dorsal valve, copy of figure from Etheridge (1918, pl. 40, fig. 11) × 3.5. P-R, *Heteralosia prendergastae* (Coleman), from Cundlego Formation, Carnarvon Basin, holotype, UWA 28444a, shell in ventral, dorsal and posterior views, × 3. S-V, *Heteralosia* sp. A, all from Madeline Formation, Carnarvon Basin. S, CPC 24441, ventral valve in dorsal view, × 2.8. T, CPC 24444, ventral valve in dorsal view, × 3. U, CPC 24442, ventral valve in dorsal view, × 3. V, CPC 24443, ventral valve in dorsal view, × 3. W-Z, AA-BB, *Heteralosia* sp. B, all from Lightjack Formation, Canning Basin. W, CPC 24450, dorsal valve in ventral view, × 2.5. X, CPC 24448, dorsal valve in ventral view, × 2.5. Y, CPC 24449, dorsal valve in ventral view, × 2.5. Z, CPC 24447, dorsal valve in dorsal view, × 2.5. AA, CPC 24445, ventral valve in dorsal view, × 2.5. BB, CPC 24446, dorsal valve in ventral view, × 2.5.

1967 *Etheridgina muirwoodae* Prendergast; Condon, p. 169

LECTOTYPE: Entire specimen on AMF 16699 (designated herein as AMF 16699a), chosen by Coleman (1957, p. 109), from Mount Marmion, West Kimberley District; Noonkanbah Formation.

MATERIAL, LOCALITY AND AGE: The syntypic series described by Etheridge (1918) was reexamined. The incomplete dorsal valve figured by Etheridge (1918, pl. 40, fig. 11) has been lost—the specimen was not available to either Prendergast (1943) or Coleman (1957). The syntypic series and specimens previously available to Etheridge (Etheridge, 1915) came from Mt Marmion, West Kimberley District, Canning Basin (see also Glauert, 1926), now included in the upper part of the Noonkanbah Formation. Coleman (1957) also recorded and figured specimens from several localities from the Wandagee Formation, Carnarvon Basin. They were well described and figured (Coleman, 1957, p. 110, pl. 17, figs 6, 10, 11) and are conspecific with the Mount Marmion material. Measurements of the species are provided by Coleman (1957, p. 110). Late Baigendzhinian (Late Artinskian).

DIAGNOSIS: Small *Heteralosia*, adherent by most of ventral valve and by coarse, long, adherent, ventral spines. Well-developed interareas, teeth, elevated, internally-bilobed cardinal process and dorsal median septum.

DESCRIPTION: Shell small, subquadrate to transversely oval in outline. Hinge width varies from just over half maximum width up to seven-eighths maximum width. Hinge extremities become pointed in mature samples, with suggestion of small ears being developed, rounded in submature, younger specimens. Ventral valve firmly fixed to underlying substrate (in all known samples, a larger brachiopod) with entire visceral disc being attached. Lateral and anterior margins of ventral valve free, being sharply upturned, not attached. Ornamentation of ventral valve consists of spines distributed along cardinal, lateral and anterior margins; number of spines variable. Spines relatively coarse, adherent to host shell, longer than shell on some specimens.

Interareas prominent, flat, extend full width of hinge; also relatively high. Ventral interarea may vary between being perpendicular to, or parallel to, plane of attachment, variation being caused by degree to which umbo itself is attached to substrate. Umbo minute, barely noticeable. Ventral interarea bisected by relatively-wide delthyrium filled by pseudodeltidium which is only slightly raised above level of interarea. Dorsal interarea half height of that of ventral interarea, flat to gently concave; bisected by notothyrium filled by triangular chilidium. Both interareas lie in one plane.

Ventral valve teeth usually strong, divergent. Diductor muscle scars large, smooth, lobate, bisected by low ridge or median septum. Adductor scars poorly differentiated. Anterior of interior of ventral valve finely pustulose, posterior cardinal margins carry numerous pits arranged in two, ill-defined rows.

Dorsal valve thin, gently concave to flat. Fine growth lamellae may be present. Valve may reflect exteriorly ornament of substrate shell—the lectotype reflects ornament of ribs of piece of *Neospirifer* sp. which acts as substrate of specimen. Dorsal valve without spines. Cardinal process prominent, exteriorly trilobed (*fide* Prendergast 1943), interiorly bilobed; inclined at almost right angle to dorsal interarea. Median septum short, fine, extends from base of process; bisects muscle field (Prendergast 1943) or, apparently, weakly dendritic (Etheridge 1918, pl. 40, fig. 11). Brachial ridges unknown.

DISCUSSION: The above description is based on a reexamination of Etheridge's (1918) syntypic series of *H. complectens* and, particularly for details of the dorsal valve, descriptions of the species by Prendergast (1943) and Coleman (1957) as well as Etheridge's (1918) illustration of the now missing syntypic dorsal valve. Etheridge's (1918) name for the species was suppressed by both Prendergast (1943) and Coleman (1957) who both mistakenly confused this small strophalosiid with *Etheridgina*, a productidinid. The fact that Etheridge (1918) used the same trivial name, *complectens*, for his adherent strophalosiid as he had used for his adherent productidinid some 50 years previously (Etheridge 1876, 1878) appears to have added to the confusion but Etheridge (1918) presumably did not refer to his adherent productidinid as he considered the two were not closely related. Etheridge's (1918) specific name *Strophalosia* (now *Heteralosia*) *complectens* is restored and its clear strophalosiid affinity is indicated, as shown by Etheridge and implied by Prendergast (1943) and Coleman (1957) and also indicated by Clarke (1970a) and Grant (1976). Waterhouse (1959) and Muir-Wood and Cooper (1960) reconfirmed the productidinid relationship of *Etheridgina* as shown by Etheridge (1876, 1878).

Heteralosia complectens is readily distinguished from other West Australian species of the genus by its smaller size, largely-adherent ventral valve and long, adherent, ventral spines. The substantial area of the ventral valve that is adherent and the long adherent spines also readily distinguish the species from the small *H. haerens* Grant (1976) from limestones of approximately similar age from Southern Thailand. *H. hystricula* Girty as figured by Cooper and Grant (1975, pl. 195) is a larger species than *H. complectens* with finer spines, less-adherent ventral valve and lower interareas; it comes from the Late Wordian and Roadian of Texas. *H. magnispina* Cooper and Grant (1975) from the Kazanian of Texas has much lower interareas than *H. complectens* but is also strongly adherent. The two Texan species are probably convergent with *H. complectens* in terms of their adherent ventral valves.

Heteralosia sp. A
Fig. 4S-V

MATERIAL, LOCALITY AND AGE: CPC 24441-24444, four small ventral valves attached to the dorsal valve of *Wyndhamia* sp. nov. specimen from BMR locality WB11, 2.4 km on a bearing of 143° from Mount Madeline, upper part of Madeline Formation, Carnarvon Basin. Early Baigendzhinian (Late Artinskian).

MEASUREMENTS (in mm): e = estimate

Specimen	Maximum width	Hinge width	Ventral height
CPC 24441	9.6	7.1	8.0
CPC 24442	7.6	4.8e	5.5+
CPC 24443	6.4	4.3e	5.5
CPC 24444	4.8	–	3.9

COMMENTS: The four small ventral valves, adherent to the host shell for much of their valves by means of long, fine adherent spines indicate a species close to *Heteralosia complectens* (Etheridge, 1918). Differences from that species are indicated by the fineness of the adherent spines and the low ventral interarea with a small, inconspicuous delthyrium and pseudodeltidium on even the largest specimen.

There is always a possibility that poorly known, small species referred to *Heteralosia* may simply be juvenile spats of large strophalosiid species (Waterhouse, 1981, p. 67) but, for the present, the four specimens appear to represent a distinctive adherent species of *Heteralosia*.

Heteralosia sp. B
Fig. 4W-Z, AA-BB

1907 *Strophalosia* sp. Etheridge, p. 7, pl. 6, fig. 8; pl. 7, figs 2-4
1958 *Strophalosia* (*Heteralosia*) *prendergastae*: Guppy *et al.*, p. 53
1958 *Etheridgina muirwoodae:* Guppy *et al.*, p. 53.

MATERIAL, LOCALITY AND AGE: CPC 24445-24450, one incomplete ventral valve and five incomplete dorsal valves from BMR locality CR 1133, Lat. 19°09′51″S, Long. 125°59′57″E, Lightjack Formation, Canning Basin. Middle Kungurian.

MEASUREMENTS (in mm):

Specimen	Maximum width	Hinge width	Ventral height	Dorsal height
CPC 24445	13.9	6.6	13.4	–
CPC 24446	15.5	10.6	–	13.4
CPC 24447	13.8	6.7	–	11.8
CPC 24448	12.8	8.2	–	11.2
CPC 24449	12.4	6.8	–	11.8
CPC 24450	12.6	7.8	–	10.7

COMMENTS: The specimens, all of variable preservation, indicate a large species of *Heteralosia* that was attached only during its early ontogenetic stages. The ventral valve carries numerous fine spines that were erect anteriorly (judging from the spine bases). The ventral interarea is distinct and carries a narrow triangular delthyrium filled with a poorly-known pseudodeltidium. The ventral valve is strongly convex. The dorsal valve is weakly convex posteriorly, flattish medianly and strongly concave and geniculate anteriorly. The median septum is half the length of the valve, sharp, thin and arises at the base of an erect, blunt, weakly-bilobed cardinal process. An internal marginal ridge is developed anteriorly preceding the pronounced geniculation of the valve.

The material can be compared with the poorly-known *Strophalosia* sp. of Etheridge (1907, pl. 6, fig. 8; pl. 7, figs 2-4) from correlatable strata (the Lower Marine Beds of the Port Keats Group) in the Bonaparte Gulf Basin. Etheridge's specimens have not been located; they are not in the South Australian Museum which houses many other specimens of his 1907 work. The illustrations provided by Etheridge indicate a species with a circular outline, finely-spinose ventral valve and a dorsal valve with a fine, sharp, median septum and an anteriorly-developed marginal ridge. Etheridge's (1907) *Strophalosia* sp. is therefore included within my *Heteralosia* sp. B.

Comparison with other Western Australian species of *Heteralosia* is hampered by the poor preservation of the material but *Heteralosia* sp. B is apparently the species indicated by Guppy *et al.* (1958) in the two citations in the synonymy quoted above.

Genus **Echinalosia** Waterhouse, 1967
= **Multispinula** Waterhouse, 1966, *non* Rowell, 1962

TYPE SPECIES: *Strophalosia maxwelli* Waterhouse, 1964.

DIAGNOSIS: Concavo-convex strophalosiids, circular to elongate in outline. Dorsal valve with trail not thickened. Ventral spines erect and semi-recumbent; dorsal spines finer than ventral spines and erect (modified from Waterhouse 1969, p. 29).

DISCUSSION: This genus is usefully separated from *Wyndhamia* Booker (1929) by details of shell outline and the dorsal valve. Two strophalosiid species from Western Australia belong in *Echinalosia*. Clarke (1970a, p. 20 and p. 21) considered that *Strophalosia prideri* Coleman might be an *Orthothrix*. *Orthothrix* Geinitz (1847a, 1847b) lapsed until reestablished by Muir-Wood and Cooper (1960) and is restricted to small strophalosiids with a trigonal posterior outline to the shell, fine, long, recumbent spines on the ventral valve and minute spines on the dorsal valve. Waterhouse (1969) referred *Strophalosia prideri* to *Echinalosia* and that assignment is followed herein. Nevertheless, the dorsal spines of *Strophalosia prideri* are much coarser than those of *Strophalosia maxwelli* Waterhouse (1964) as noted by Clarke (1970a). The genus morphologically closest to *Echinalosia* is *Marginalosia* Waterhouse (1978a, p. 64) with ?*Echinalosia kalikotei* Waterhouse (1975) as type species. *Marginalosia* possesses erect spines on the ventral valve (finer than on *Echinalosia*) and a thick marginal ridge on the interior of both valves (see Waterhouse 1978a, for full discussion).

DISTRIBUTION: *Echinalosia* is abundant in the Permian faunas of New Zealand and Eastern Australia (Waterhouse 1966, 1969, Dear 1971, Clarke & Farmer 1976), present in the Permian of Western Australia and present in the Himalayas (Waterhouse 1966, Chang & Ching 1976) and probably the Salt Range (as discussed by Waterhouse, 1966). The genus has been described from Arctic Canada (Waterhouse, 1969) and is possibly present in north-eastern Siberia in the form *Strophalosia*? *bajkurica* Ustritskiy as summarised and referred to *Strophalosia* by Grigor'eva (1977). *Strophalosia inexpectans* Cooper and Grant (1975) from the Guadalupian of Texas may be an *Echinalosia*; however, the generic


A
B
C
D
E
F
K
G
I
J
L
H
N
O
U
M
P
R
V
Q
S
T
W
X
Y
Z

diagnosis may have to be modified to incorporate a form with such fine spines. *Echinalosia* also appears to be present in Kungurian faunas of the Ussuriland (in the form of *Strophalosia*? *paradoxa* Frederieks 1925).

Two subgenera are recognised within the genus, as discussed below. *Echinalosia prideri* (Coleman) is retained within the nominal subgenus.

Echinalosia (Echinalosia) prideri (Coleman, 1957)
Fig. 5A-Z

1943 *Strophalosia jukesi* Prendergast, p. 47, pl. 5, figs 18-20
1957 *Strophalosia prideri* Coleman, p. 116, pl. 18, figs 15, 16; pl. 19, figs 1-19
1967 *Strophalosia prideri* Coleman, Condon, p. 149
1976 *Strophalosia prideri* Coleman, Waterhouse, p. 99

Holotype: CPC 1018, complete shell, from right bank of Lyndon River, 14.4 km east of Mia Mia Homestead, Carnarvon Basin. Originally mapped as Bulgadoo Shale; subsequently mapped as Madeline Formation.

Material, Localities and Age: CPC 24497a-24497e, three shells and two isolated dorsal valves from BMR locality ML87, 13.6 km on a bearing of 82° from Mia Mia Homestead, north bank of Lyndon River, Madeline Formation. CPC 24498a-24498e, two shells and one isolated dorsal valve from BMR locality ML88, as for ML87, middle fossiliferous horizon, Madeline Formation. CPC 24415, 24416, 24499a-24499b, four shells from BMR locality F17721, 14.4 km east of Mia Mia Homestead, right bank of Lyndon River, type locality of species, Madeline Formation. CPC 24417, 24500a-24500b, two internal moulds of complete shells and one ventral valve internal mould from BMR locality WB51, 3.6 km on a bearing of 225° from Keogh Hill, lower part of Madeline Formation. All Carnarvon Basin. All Early Baigendzhinian (Late Artinskian).

Size Ranges: Ranges are based on 38 measured specimens (including the 15 figured specimens). Hinge width, 11.1-26.8 mm; maximum width 16.4-51.0 mm; ventral valve height, 13.8-42.9 mm; dorsal valve height 11.4-36.8 mm; thickness, 11.6-19.5 mm (based on 6 specimens—most are crushed); ventral interarea height, 1.8-4.8 mm; dorsal interarea height, 1.2-2.6 mm; dorsal septum length, 9.0-15.0 mm (based on 8 specimens).

Diagnosis: Large *Echinalosia*, transversely oval to subtrigonal in outline. Ventral valve with convexity accentuated towards margins and with median flattening, rarely with broad shallow sulcus anteriorly in large specimens. Ventral spines abundant, coarse and erect; dorsal spines scattered and relatively coarse. Ventral umbo prominent and pointed; hinge narrow in mature specimens.

Description: Shell large for genus, outline varies from transversely oval or subcircular in juvenile specimens to transversely subtrigonal in mature specimens. Ventral valve strongly convex with convexity being more pronounced towards lateral margins. Ventral valve may be medianly flattened, in a few adult specimens carries broad, flattened, relatively inconspicuous sulcus anteriorly. Ventral convexity more accentuated over visceral disc, decreases anteriorly along trail. Hinge line straight, up to two-thirds maximum shell width in juvenile shells, normally less than half maximum width in adults. Maximum shell width anterior of mid-length of shell. Cardinal region of shell imparts prominent triangular appearance to shell posterior with effect increased in many specimens by posterior lateral margins of valves being straight, parallel to umbonal shoulders; resulting in a distinct subtrigonal outline to many specimens. Small, pointed ears may be developed on some specimens—others lack them entirely. Ventral umbo variable in shape; normally pointed, suberect, with small cicatrix, on some specimens incurved, overhangs ventral interarea. Ventral interarea prominent, triangular; height highly variable, striated parallel to hinge and, less distinctly, parallel to shell length. Small, high, extremely narrow delthyrium bisects interarea, filled by strongly-convex pseudodeltidium.

Exterior ornamentation of ventral valve consists of spines, concentric growth lamellae; lamellae consist of well-spaced major lamellae and closely-set (often worn, removed) fine growth lines. Spines developed as row along hinge, subconcentric rows across venter of shell. Spacing of spines a little closer over lateral margins of valve than across valve centre. Lateral spines tend to be suberect, point laterally and posteriorly. Remainder of ventral spines erect, point anteriorly. Lateral spines grade into venter spines, no discrete demarcation occurs between them. Spines vary in coarseness over valve but may be up to 1 mm thick with spine bases up to 1.5 mm thick. Some spines on anterior of largest shells may be fine (0.6 mm wide), adjacent to coarser spine. Normally about 14 spines per cm^2 at 2-3 cm from umbo, spaced every 4 to 7 mm along concentric row. Body spines apparently quite long, longest measured being 5 mm.

Exterior ornament of dorsal valve consists of distinct, relatively widely spaced, concentric growth lamellae, numerous spines (finer than those of ventral valve) and

Fig. 5—A-Z, *Echinalosia* (*Echinalosia*) *prideri* (Coleman). All from Madeline Formation, Carnarvon Basin. A-B, CPC 24497a, shell in dorsal and ventral views, × 1.2 and × 1.3 respectively. C-D, CPC 24498a, shell in dorsal and ventral views, × 1.3 and × 1.2 respectively. E-F, CPC 24498b, shell in dorsal and ventral views, × 1.2. G-H, CPC 24499a, shell in ventral and dorsal views, × 1.2. I-J, CPC 24499b, shell in ventral and dorsal views, × 1. K-L, CPC 24416, shell in dorsal and ventral views, × 1. M-O, CPC 24497b, shell in ventral, dorsal and lateral views, × 1.2. P-Q, CPC 24500a, internal mould of shell in ventral and dorsal views, × 1.2. R, CPC 24500b, internal mould of ventral valve, × 1.2. S, CPC 24498c, dorsal valve interior view, × 1.1. T, CPC 24497e, dorsal valve interior view, × 1.1. U-V, CPC 24415, shell in ventral and dorsal views, × 1 and × 1.2 respectively. W, CPC 24497d, dorsal valve interior view, × 1.1. X, CPC 24497e, decorticated shell in dorsal view, × 1.2. Y-Z, CPC 24417, internal mould of shell in ventral and dorsal views, × 1.1.

scattered subcircular dimples. Spines arranged in concentric rows, may be up to 0.7 mm thick at their base, erect, up to 5 mm long. Decortication of valve removes most spines, leaves coarser concentric lamellae and widely scattered dimples. Dimples tend to be circular to subcircular (slightly longer than wide), normally scattered along concentric rows. Capillae have not been observed on best preserved specimens.

Ventral teeth strong, robust, divergent but set relatively close together because of narrow delthyrium. Low marginal ridge developed either side of teeth, persists anteriorly in only mature specimens as low, broad ridge around anterior perimeter of valve. Adductor muscle scars elongate, on a raised platform; normally bisected by median groove, although one specimen shows median ridge, smooth or feebly striate longitudinally. Diductor scars large, flabellate, weakly impressed anteriorly, posteriorly smooth, anteriorly striate, extend further anteriorly than adductor scars. Remainder of valve interior smooth or finely pitted.

Dorsal valve smoothly geniculate with geniculated angle being curved up to about 40° from anterior of gently internally-convex visceral disc. Dorsal interarea distinct, high, striated parallel to hinge line; bisected by sharply concave chilidium, wider than corresponding pseudodeltidium. Dorsal adductor scars smooth, bisected by median septum so that each half triangular shaped. Anterior components of adductor scars raised above level of visceral disc, posterior components depressed, lower than level of visceral disc. Brachial ridges distinct in mature specimens, arise close to anterior of posterior components of adductor scars; broadly semicircular, hook back sharply at their anterior extremities. Region of brachial ridges smooth. Cardinal process strong, erect, extends behind hinge line, coplanar with dorsal interarea or diverges posteriorly by some 10-15°. Process quadrilobed interiorly, prominent median lobe divided by deep groove; lateral lobes of process distinct, project widely from bisected median lobe. Cardinal process arises from strongly-developed median septum and a pair of low marginal ridges that run around deep sockets and die out on lateral margins of valve. Median septum strong, sharp, high (usually lower between adductor scars), extends for about half valve length. Anterior of valve interior distinctly pustulose.

Discussion: *Echinalosia prideri* was well described by Coleman (1957) who also discussed such features as the variable nature of the ventral umbo and the height of the ventral interarea. The new material to hand indicates few changes to Coleman's description of the species. The ventral umbo can rarely be overturned over the interarea and one juvenile specimen indicates that the cicatrix can rarely attain a large size (just over 0.5 cm at the largest diameter).

Echinalosia sp. (Waterhouse 1969) from Arctic Canada is a large form differing from *Echinalosia prideri* in possessing a distinct sulcus, more densely-spinose ventral valve and a wider hinge line.

Eastern Australian species of *Echinalosia* such as *E. preovalis* (Maxwell 1954, pl. 54, figs 1-19) and *E. ovalis* (Maxwell 1954, pl. 57, figs 4-14) are more circular species than *E. prideri* and possess relatively wide hinges (see also Dear 1971, pl. 3, figs 11-16, *Echinalosia minima* Dear 1971).

The same is also true of *Echinalosia* from New Zealand as described and figured by Waterhouse (1964). Waterhouse (1982a, see p. 31 for synonymy) has reported in many papers that *E. prideri* is a characteristic zone fossil of Mangapirian (Late Artinskian) faunas of New Zealand. However, specimens of the New Zealand form are limited in number and preservation and only one specimen has been figured (Waterhouse 1982, pl. 23, fig. i). The figured specimen is an internal mould of a ventral valve which may indicate a species related to *E. prideri* but until the dorsal valve of the New Zealand species is known and larger collections are available, the identity of the species is in considerable doubt.

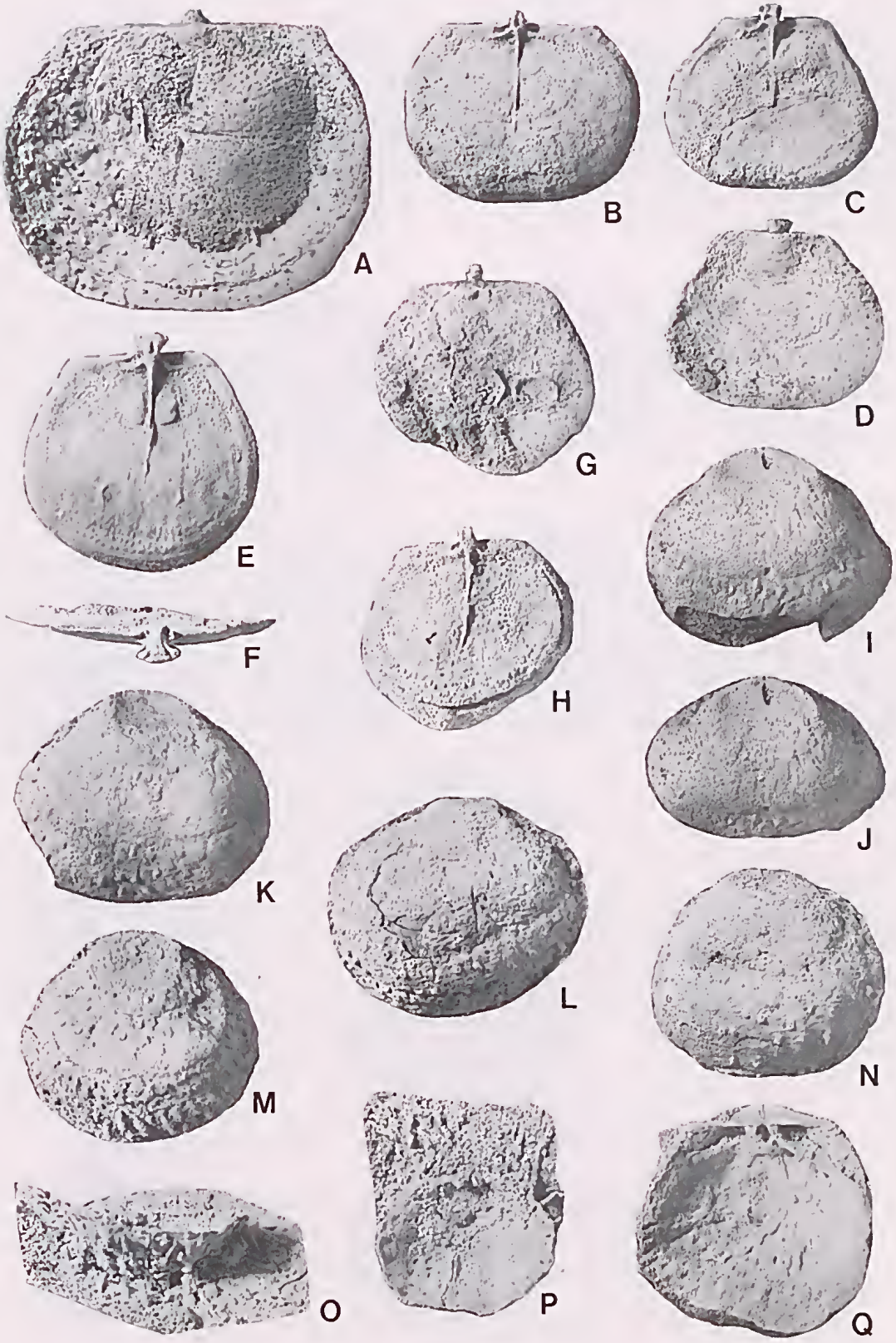
Subgenus **Echinalosia (Notolosia)** subgen. nov.

Type Species: *Echinalosia* (*Notolosia*) *dickinsi* sp. nov.

Diagnosis: Concavo-convex strophalosiids with circular to subcircular outline. Shell not thickened. Cicatrix large. Ventral spines adherent, semi-recumbent and erect. Dorsal spines erect, minute and abundant. Ventral interarea relatively high with high but narrow pseudodeltidium. Teeth small. Cardinal process high, erect, with prominent bisecting groove and pit on interior face; quadrilobed at maturity.

Discussion: Specimens of the type species have previously been referred to *Heteralosia* (Coleman 1957) but larger collections show that the species possesses numerous minute, scattered, dorsal spines unlike that genus. Slight erosion of the dorsal valve removes all trace of the spines but leaves the lamellose growth lines. The species shares many features with *Echinalosia* Waterhouse and hence is placed in that genus but characters such as the large cicatrix and long, adherent spines indicate considerable differences from *E. maxwelli* (Waterhouse 1964) the type species of *Echinalosia*, hence the new subgenus is proposed.

Fig. 6—A-Q, *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. All from Hardman Formation, Canning Basin. A-B, CPC 24451, holotype, dorsal valve in dorsal and ventral views, × 3 and × 2 respectively, with attached internal mould of *Neochonetes* (*Sommeriella*) sp. nov. C-D, CPC 24452, dorsal valve in ventral and dorsal views, × 2.2 E-F, CPC 24453, dorsal valve in ventral and posterior views, × 2 and × 3 respectively. G-H, CPC 24454, dorsal valve in dorsal and ventral views, × 2.2. I-J, CPC 24468, natural cast of ventral valve in ventral and posterior views, × 1.5. K, CPC 24469, natural cast of ventral valve in ventral view, × 1.6. L, CPC 24470, natural cast of ventral valve in ventral view, × 1.8. M, CPC 24471, natural cast of ventral valve in ventral view, × 1.8. N, CPC 24472, natural cast of ventral valve in ventral view, × 1.6. O-P, CPC 24460, ventral valve in anterior and dorsal views, × 2.8 and × 2.6 respectively. Q, CPC 24462, ventral valve adherent within ventral valve, × 3.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

Echinalosia (*Echinalosia*) Waterhouse (1967) is a larger subgenus of subtrigonal or subcircular outline and with scattered dorsal spines. Internal features such as muscle scars and brachial ridges are more strongly developed in *Echinalosia* (*Echinalosia*), which also has a consistently, considerably smaller cicatrix of attachment than *Echinalosia* (*Notolosia*) subgen. nov. No other species is at present referable to *Echinalosia* (*Notolosia*).

Orthothrix Geinitz (1847a, 1847b) is a smaller genus with numerous, minute dorsal spines but is characterised by a trigonal outline, fine recumbent ventral spines, a short dorsal median septum and a less convex ventral valve.

Wyndhamia Booker (1929) possesses fine dorsal spines but at maturity, shells are large and subquadrate in outline. There is no evidence at present to suggest that *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. is only known from juvenile material. Large strophalosiids occur with representatives of the species but they are representatives of a large new genus that lacks dorsal spines and that will be described in a subsequent study.

Echinalosia (Notolosia) dickinsi sp. nov.
Figs 6A-Q, 7A-S

1957 *Strophalosia* (*Heteralosia*) *prendergastae* Coleman, (partim.), p. 127, pl. 20, figs 29-35, (non cet.)

1958 *Strophalosia* (*Heteralosia*) *prendergastae* Coleman, Guppy *et al.*, p. 54

1961 *Strophalosia* sp. Dickins, pp. 284, 287

Etymology: For Dr J. M. Dickins of the Bureau of Mineral Resources, Geology and Geophysics, for his extensive contributions to the knowledge of the Western Australian Permian record.

Holotype: CPC 24451, an isolated dorsal valve from BMR locality KLB 11, Hardman Formation, Canning Basin.

Material, Localities and Age: CPC 24451-24467, nine isolated dorsal valves and eight isolated ventral valves from BMR locality KLB 11, Mount Hardman, from beds about 1.2 m thick at about 40 m below the top of the hill, Hardman Formation. CPC 24468-24472, five natural casts of ventral valves from BMR locality N1241, Lat. 19°06′39″S, Long. 125°11′27″E, Hardman Formation, Canning Basin. Chhidruan (Early Tatarian).

Size Ranges: e = estimate. Ranges are based on 34 measured specimens (including the 22 figured specimens). Hinge width, 5.8-15.5e mm; maximum width, 10.1-26.5 mm; ventral valve height, 8.8-22.5 mm; dorsal valve height, 9.8-20.0 mm; thickness, 3.5-12.1 mm; ventral interarea height, 1.1-2.8 mm; dorsal interarea height, 0.6-1.5 mm; dorsal septum length, 5.5-11.6 mm.

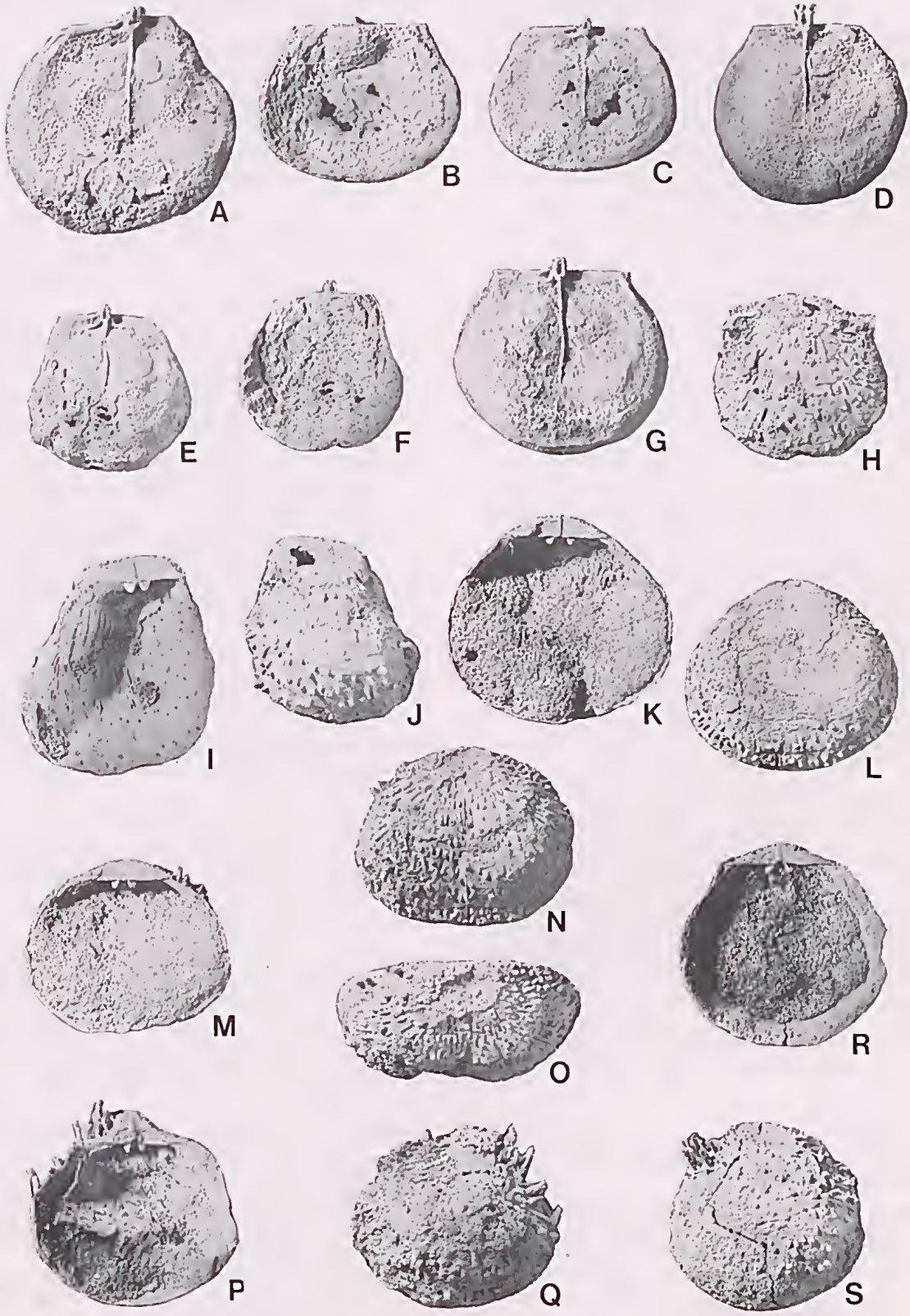
Diagnosis: Small to medium sized shells with narrow hinge line and transversely oval outline in maturity. Cicatrix large. Ventral exterior ornament of concentric lamellae and fine, abundant, scattered to subconcentrically arranged spines. Dorsal exterior with minute scattered spines, scattered dimples, and concentric growth lamellae.

Description: Shell of moderate size with transversely oval outline at maturity. Hinge width varies from two-thirds of maximum width in juvenile stages of ontogeny to one half maximum width at maturity. Hinge extremities rounded at maturity, finely pointed in juvenile specimens. No ears developed. Ventral valve strongly convex with convexity being even. Maximum width at about two-thirds of length of shell, from umbo, at maturity. Umbo flattened by cicatrix of attachment which is large in size (largest being on specimen CPC 24468, 8.7 mm wide 7.3 mm long). Ornamentation of ventral valve consists of spines and concentric lamellae with the latter widely spaced and best seen on anterior of valve. Spines closely spaced, numerous, those over posterior lateral flanks more closely spaced than those over venter. No distinct row developed along hinge, although spines extend up to hinge. Cicatrix occupies large portion of umbonal and posterior hinge region. Spines spaced at 1 to 2 mm intervals over venter in subconcentric bands and are from 0.2 to 0.4 mm thick. Larger specimens appear to have coarser spines anteriorly but this may in part be because of nature of preservation (as natural ferruginous casts). Posterior spines adherent to substrate, although they are long and lift juvenile shell from substrate (specimen CPC 24460).

Interareas distinct, flat, extend full width of hinge, relatively high. Ventral interarea striated parallel to hinge, bisected by narrow, triangular delthyrium filled by flat pseudodeltidium. Pseudodeltidium inconspicuous when entire. Dorsal interarea about half height of ventral interarea, weakly striate parallel to hinge line, bisected by narrow, flat chilidium.

Dorsal valve flat or gently convex during earliest stages of ontogeny, becomes gently concave subsequently. Anterior of dorsal valve distinctly, but not sharply, geniculated. Concentric lamellae distinct. Dimples scattered over valve surface. Concentric lamellae and growth lines carry rows of minute spines (up to 0.6 mm apart and 0.2 mm thick). Spines may be totally removed from valve without loss of lamellae.

Fig. 7—A-S, *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. All from Hardman Formation, Canning Basin. A, CPC 24455, dorsal valve in ventral view, × 2. B-C, CPC 24456, dorsal valve in dorsal and ventral views, × 2.8 and × 2.5 respectively. D, CPC 24457, dorsal valve in ventral view, × 2. E-F, CPC 24458, dorsal valve in ventral and dorsal views, × 2.6. G, CPC 24459, dorsal valve in ventral view, × 2.2. H, CPC 24462, ventral valve in ventral view, × 2.2. I-J, CPC 24463, ventral valve in dorsal and ventral views, × 3 and × 2.5 respectively. K-L, CPC 24464, ventral valve in dorsal and ventral views, × 1.5. M-O, CPC 24465, ventral valve in dorsal, ventral and posterior views, × 1.6, × 1.8, and × 2 respectively. P-Q, CPC 24466, ventral valve in dorsal and ventral views, × 2. R-S, CPC 24467, ventral valve in dorsal and ventral views, × 1.8.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
R
P
Q
S

Ventral teeth small, weakly divergent, protrude from under ventral interarea. No marginal ridge developed. Adductor scars situated high under umbo, smooth and lobate. Diductor scars poorly known but appear weakly striate.

Cardinal process arises from strong median septum and two minute lateral ridges which surround small but narrow and deep sockets. Process a small, bilobed spike in juvenile specimens and a pronounced quadrilobed, erect eminence in mature valves. It extends posteriorly at small angle to plane of dorsal interarea.

Smooth dorsal adductor scars distinct, particularly in mature specimens, and raised above level of visceral disc; bisected by median septum, not differentiated into anterior and posterior components even in largest specimen. Median septum usually from 0.5 to 0.6 length of dorsal valve, thin and sharp. Abundant papillae occur around anterior of valve. Brachial ridges only weakly developed in largest dorsal valve.

Discussion: Several small specimens of this species, figured by Coleman (1957, pl. 20, figs 29-35) as *Heteralosia prendergastae* are referred to *E.* (*N.*) *dickinsi* sp. nov. on the basis of ventral spinosity, cicatrix type and dorsal interior. Dickins (1061) recorded *Strophalosia* sp. from the Hardman Formation which appears to refer to the present species. *Echinalosia* (*Notolosia*) *dickinsi* sp. nov. is a distinctive species because of its large cicatrix, ventral spine arrangement and minute dorsal spines. Comparison may be suggested with representatives of *Echinalosia* (*Echinalosia*), but in addition to comments noted above, that subgenus possesses dorsal adductor scars that are differentiated into anterior and posterior components, unlike the present species.

ACKNOWLEDGEMENTS

Dr J. M. Dickins, Bureau of Mineral Resources, Geology and Geophysics; Dr A. E. Cockbain, Geological Survey of Western Australia; Mr D. Rhodes, Department of Geology, University of Western Australia; Dr A. Ritchie and Mr R. Jones, the Australian Museum and Dr G. A. Thomas, Department of Geology, University of Melbourne are all thanked for the loan of specimens. This study was completed while the author was an Associate of the Department of Geology, University of Melbourne.

Dr G. A. Thomas read an earlier version of the manuscript; Mrs I. Munro typed the manuscript and Mrs L. Archbold assisted with photography.

REFERENCES

References are supplementary to those in Part 1-5 (*Proc. R. Soc. Vict.* vol. 91, p. 181; vol. 93, p. 109; vol. 95, p. 237; vol. 96, p. 83; vol. 97, p. 19).

Archbold, N.W., 1985. Studies on Western Australian Permian brachiopods 5. The family Dictyoclostidae Stehli 1954. *Proc. R. Soc. Vict.* 97: 19-30.

Archbold, N.W. & Thomas, G.A., 1985. New genera of Western Australian Permian Spiriferidae (Brachiopoda). *Alcheringa* 9: 269-292.

Booker, F.W., 1929. Preliminary note on new subgenera of *Productus* and *Strophalosia* from the Branxton district. *J. R. Soc. N.S. Wales* 63: 24-32.

Clarke, M.J., 1970a. Tasmanian Strophalosiidae. *Rec. geol. Surv. Tasmania* 10: 1-51.

Clarke, M.J. & Farmer, N., 1976. Biostratigraphic nomenclature for Late Palaeozoic rocks in Tasmania. *Pap. Proc. R. Soc. Tasmania* 110: 91-109.

Cooper, G.A. & Stehli, F.G., 1955. New genera of Permian brachiopods from West Texas. *J. Paleontol.* 29: 469-474.

Davidson, T., 1853. British Fossil Brachiopoda. 1. A General Introduction. *Palaeontographical Soc. Mono.* 136 p.

Dickins, J.M., 1961. Mesozoic and Permian fossils from the Canning Basin. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 60: 282-288.

Etheridge, R., 1876. On an adherent form of *Productus* and a small *Spiriferina* from the lower Carboniferous Limestone Group of the east of Scotland. *Q. Jl. geol. Soc. Lond.* 32: 454-465.

Etheridge, R., 1878. Further remarks on adherent Carboniferous Productidae. *Q. Jl. geol. Soc. Lond.* 34: 498-504.

Etheridge, R., 1907. Official contributions to the Palaeontology of South Australia. *South Aust. Parl. Pap.* (*Blue Book*) 1907, 54: 3-21.

Etheridge, R., 1915. Western Australian Carboniferous fossils chiefly from Mt Marmion, Lennard River, West Kimberley. *Bull. geol. Surv. W. Aust.* 58: 1-59.

Everest, R., 1831. Fossil shells sent down from the Himalayan mountains by Dr Gerard. *Gleanings in Science* 3: 30.

Everest, R., 1833. Memorandum on the fossil shells discovered in the Himalayan Mountains. *Asiatic Researches* 18: 107-114.

Geinitz, H.B., 1847a. *Orthothrix* Geinitz, eine neue gattung der Brachiopoden. *Korrespondenzblatt d. Zoolog.-Mineralog. Ver., Regensberg* 1847: 117-118.

Geinitz, H.B., 1847b. *Orthothrix* Geinitz, eine neue gattung der Brachiopoden. *Bull. Soc. Imp. Nat. Moscou.* 20 (2): 84-86.

Gerard, J.G., 1831. Fossil shell strata of the Himalaya. *Gleanings in Science* 3: 92-93.

Gerard, J.G., 1833. Observations on the Spiti Valley and circumjacent country within the Himalaya. *Asiatic Researches* 18: 238-278.

Glauert, L., 1926. A list of Western Australian fossils. *Bull. geol. Surv. W. Aust.* 88: 36-71.

Greger, D.K., 1920. North American species of the Brachiopod *Etheridgina*. *Geol. Mag.* 57: 535-538.

Grigor'eva, A.D., 1977. Nadsemeistvo Strophalosiacea. *Trudy Paleont. Inst., Akad., Nauk SSSR* 161: 41-53.

Guppy, D.J., Lindner, A.W., Rattigan, J.H. & Casey, J.N., 1958. The Geology of the Fitzroy Basin, Western Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 36: 1-116.

Herbert, J.D., 1831. On the organic remains found in the Himalaya. *Gleanings in Science* 3: 265-272.

Kalashnikov, N.V. & Ustritskiy, V.I., 1981. Brakhiopody. In, *Permiskie Otlozheniya Novoi Zemli*, V.I. Ustritskiy, ed., Izd-vo "Nauka", Leningrad, pp. 51-67.

King, W., 1844. On a new genus of Palaeozoic shells. *Ann. Mag. nat. Hist.* 14: 313-317.

King, W., 1845. *Allorisma*, ein neues palaozoischen Muschelgeschlecht. *Neues Jb. Mineral. Geog. Geol. Petrefakten-kunde* 16: 254-255.

KING, W., 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Ann. Mag. nat. Hist.* 18: 26-42, 83-94.

KING, W., 1847. Bemerkungen über gewisse genera aus der Klasse der Palliobranchiaten. *Neues Jb. Mineral. Geog. Geol. Petrefakten-kunde* 18: 247-254.

KING, W., 1850. A monograph of the Permian fossils of England. *Palaeontographical Soc. Mono.* 3: i-xxxvii, 1-258.

LIAO, ZHUO-TING, 1982. New genera and species of Aulostegacea (Brachiopoda). *Acta Palaeont. Sinica* 21 (5): 537-544.

LICHAREW, B.K., 1934a. Fauna Permiskikh otlozhenii Kolymskogo Kraya. *Akad., Nauk SSSR, Trudy Sov. izuchen proizvod. sil., Ser. Yakutskaya* 14 (1): 1-148.

MANANKOV, I.N. & PAVLOVA, E.E., 1976. *Mongolosia*—the new genus of Permian brachiopods. *Paleont. Biostrat. Mongolii, Trudy* 3: 354-357.

MANSUY, H., 1914. Faunes des calcaires a *Productus* de L'Indochine. *Mem. Serv. Geol. Indochine* 3 (3): 1-59.

MAXWELL, W.G.H., 1954. *Strophalosia* in the Permian of Queensland. *J. Paleontol.* 28 (5): 533-559.

MCKELLAR, R.G., 1970. The Devonian productoid brachiopod faunas of Queensland. *Publ. geol. Surv. Qld* 342, *Palaeont. Pap.* 18: 1-40.

MIRSKAYA, M.F., SHESTAKOVA, M.F. & CHUDINOVA, I.I., 1956. O nekotorykh novykh okamenelostyakh iz nizhnepermskikh otlozhenii Kamskogo Priural'ya. *Uchenye Zapiski Molotov. Gosudarst. Universiteta im A.M. Gor'kogo* 7 (4): 27-43.

ROWELL, A.J., 1962. The genera of the brachiopod superfamilies Oboleliacea and Siphonotretacea. *J. Paleontol.* 36: 136-152.

ROYLE, J.F., 1839-1840. *Illustrations of the Botany and other branches of the Natural History of the Himalayan Mountains, and of the flora of Cashmere.* 2 vols, Wm.H. Allen and Co., London.

SCHUCHERT, C., 1913. Brachiopoda. In, *Textbook of Palaeontology*, K. von Zittel, ed., (trans. & ed. by C.R. Eastman), 2nd edn., Macmillan and Co. Ltd, London. pp. 355-420.

SOWERBY, J.DEC., 1832. List of fossil shells from the Himalaya. *Jl. Asiatic Soc. Bengal.* 1: 248-249.

SOWERBY, J.DEC., 1833, List of Himalayan Fossil Shells. *Asiatic Researches* 18: 278.

WATERHOUSE, J.B., 1959. Genus *Leptalosia* Dunbar and Condra. *N.Z. Jl. Geol. Geophys.* 2 (2): 338-341.

WATERHOUSE, J.B., 1967. Proposal of series and stages for the Permian in New Zealand. *Trans. R. Soc. N. Zealand, Geology* 5 (6): 161-180.

WATERHOUSE, J.B., 1969. Permian *Strophalosiidae* (Brachiopoda) from the Canadian Arctic Archipelago. *J. Paleontol.* 43 (1): 28-40.

WATERHOUSE, J.B., 1983. Permian brachiopods from Pija Member, Senja Formation, in Manang District of Nepal, with new brachiopod genera and species from other regions. *Bull. Ind. Geol. Assoc.* 16 (2): 111-151.

WATERHOUSE, J.B., BRIGGS, D.J.C. & PARFREY, S.M., 1983. Major faunal assemblages in the Early Permian Tiverton Formation near Homevale Homestead, Northern Bowen Basin, Queensland. In, *Permian Geology of Queensland.* Geol. Soc. Aust., Qld. Div., Brisbane. pp. 121-138.

WATERHOUSE, J.B. & GUPTA, V.J., 1977. Permian faunal zones and correlations of the Himalayas. *Bull. Ind. Geol. Assoc.* 10 (2): 1-19.

WATERHOUSE, J.B. & GUPTA, V.J., 1983a. Permian brachiopod and bivalve zones in the Himalaya of India and Nepal. *Contrib. Himal. Geol.* 2: 125-129.

WATERHOUSE, J.B. & GUPTA, V.J., 1983b. A faunule from the *Lamninargus himalayensis* Zone in the Upper Shyok Valley, Southern Karakorum Range. *Contrib. Himal. Geol.* 2: 234-245.

WATERHOUSE, J.B. & SHAH, S.C., 1966. *Costalosia*, a new strophalosiid genus (Brachiopoda) from the Permian of South Asia. *Trans. R. Soc. N. Zealand, Geology* 4 (12): 229-234.